Mammalian Diversity and Matses Ethnomammalogy in Amazonian Peru

Part 4: Bats

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ABSTRACT

In this report, the fourth of our monographic series on mammalian diversity and Matses ethnomammalogy in the Yavarí-Ucayali interfluvial region of northeastern Peru, we document the occurrence of 98 species of bats, including 11 emballonurids, 2 noctilionids, 66 phyllostomids, 1 furipterid, 4 thyropterids, 7 vespertilionids, and 7 molossids. New species based on specimens collected in this region (*Peropteryx pallidoptera*, *Micronycteris matses*, *Hsunycteris dashe*, *Sturnira giannae*, and *Thyroptera wynneae*) have already been described elsewhere, but noteworthy distributional and taxonomic results newly reported here include the first specimen of *Diclidurus isabella* from Peru and the diagnosis of *Glossophaga bakeri* as a species distinct from *G. commissarisi*. Lists of examined voucher specimens, identification criteria, essential taxonomic references, and summaries of natural history observations are provided for all species. Original natural history information reported herein includes numerous observations of roosting behavior obtained by indigenous Matses collaborators.

We assess the Yavarí-Ucayali bat inventory for completeness and conclude that more species remain to be discovered in the region, where as many as 116 species might be expected. Most of the "missing" species (those expected based on geographic criteria but not actually observed) are aerial insectivores, a guild that is notoriously difficult to sample by mistnetting. Of the 98 species in the observed regional fauna, only 71 are known to occur sympatrically at Jenaro Herrera, by far the best-sampled locality between the Yavarí and Ucayali rivers. Faunal comparisons with extralimital inventories (e.g., from Brazil, Ecuador, and French Guiana) suggest that frugivorous bats are substantially more speciose in western Amazonia than in eastern Amazonia, a result that is consistent with previous suggestions of an east-to-west gradient in the trophic structure of Amazonian mammal faunas.

As previously reported, the Matses have only a single name for "bat," but they recognize the existence of many unnamed local species, which they distinguish on the basis of morphology and behavior. However, by contrast with the well-documented accuracy of Matses observations about primates and other game species, recorded Matses monologs about bat natural history contain numerous factual errors and ambiguities. Linguistic underdifferentiation of bat diversity and inaccurate natural history knowledge are both explained by cultural inattention to small, inedible, and inoffensive nocturnal fauna.

INTRODUCTION

This report is the fourth installment of a monographic series on mammalian diversity and ethnomammalogy in a sparsely inhabited region of lowland rainforest between the Yavarí and Ucayali rivers in northeastern Peru. Like others in this series (Voss and Fleck, 2011, 2017; Voss et al., 2019), the present monograph is based on specimens and observations collected over many decades, and on ethnobiological research with the Matses, a Panoan-speaking group of indigenous Amazonians with intact traditional knowledge of the local fauna (Fleck and Harder, 2000). The primary objectives of these monographs are to document the species richness of the regional mammalian fauna through taxonomic analysis of collected specimens, and to assess the extent of Matses knowledge of mammalian natural history based on recorded interviews and other ethnographic methods.

The introductory report in this series (Voss and Fleck, 2011) summarized current knowledge about the physical geography, climate, and vegetation of the Yavarí-Ucayali interfluve (figs. 1, 2), provided background information about the indigenous cultures of the region, and analyzed taxonomic and ethnographic data on primates. A second report (Voss and Fleck, 2017) provided equivalent taxonomic and ethnographic treatments for the larger mammals (Xenarthra, Carnivora, Perissodactyla, Artiodactyla, Sirenia), and a third (Voss et al., 2019) treated the regional marsupial fauna (Didelphimorphia). In this

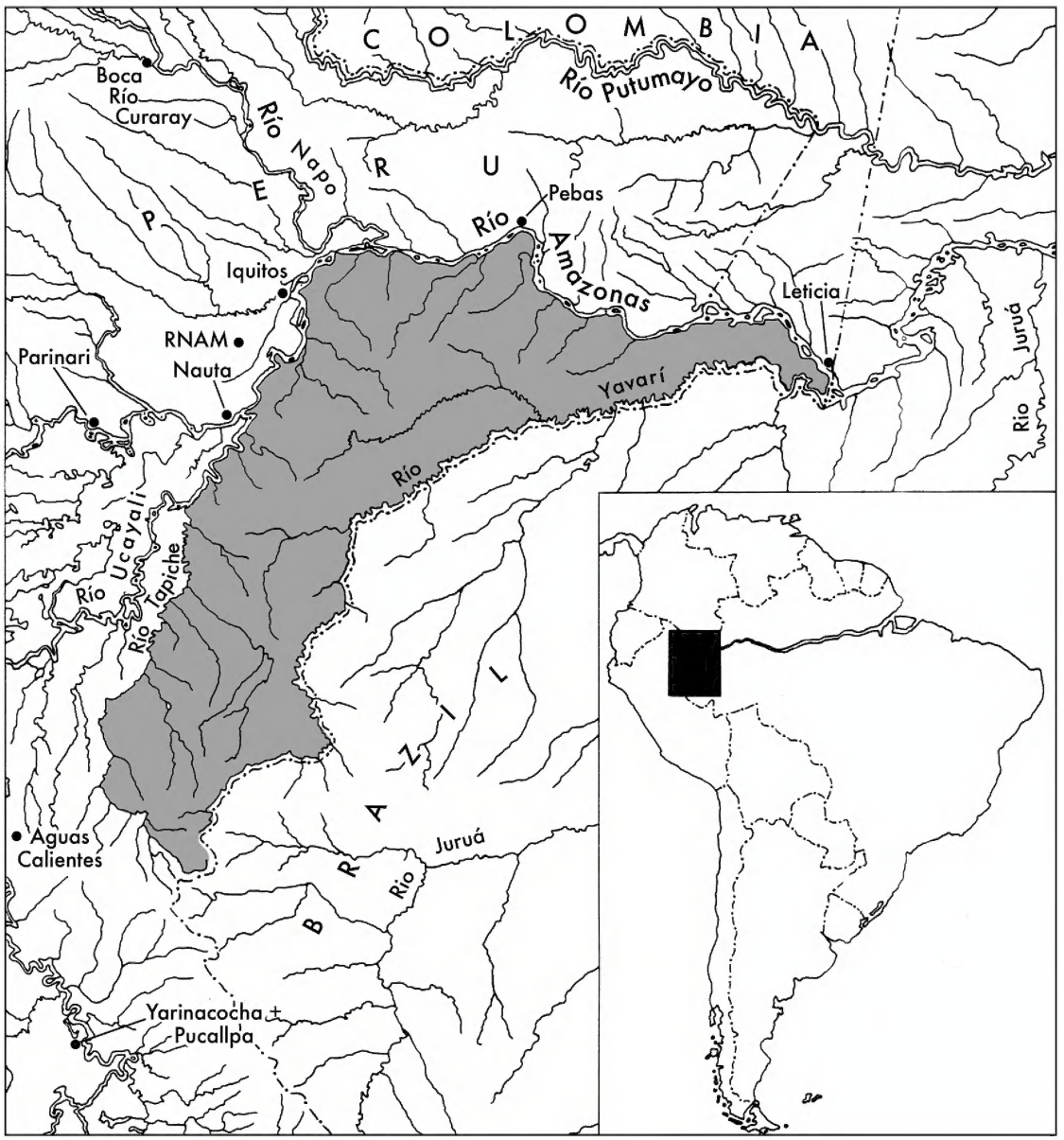


FIG. 1. The Yavarí-Ucayali interfluve (shaded) in relation to surrounding geographical features of western Amazonia. RNAM = Reserva Nacional Allpahuayo-Mishana.

report we turn to bats (Chiroptera), by far the most speciose mammalian clade in our region.

As is now widely recognized, exhaustively inventorying local bat faunas anywhere in the forested Neotropical lowlands is a logistically daunting enterprise (Voss and Emmons, 1996; Simmons and Voss, 1998; Sampaio et al., 2003; Hice et al., 2004), but the taxonomic analysis of collected specimens is scarcely less challenging. Neotropical bat taxonomy is an active field of research, especially with respect to species delimitation and nomenclature. As a result, many widespread "species" have been found to be complexes of genetically distinct

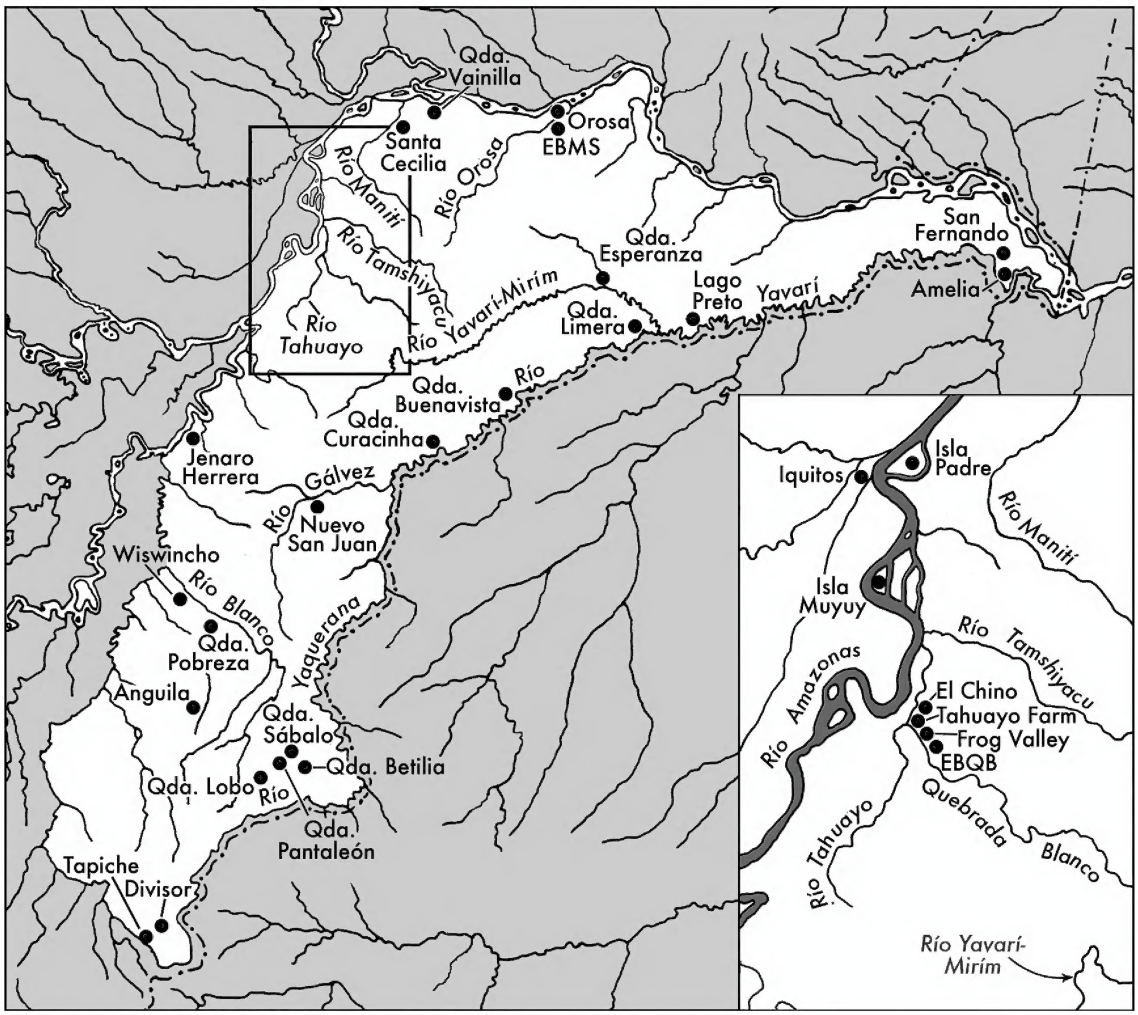


FIG. 2. Faunal inventory sites and other collecting localities within the Yavarí-Ucayali interfluve (see appendix 1 for geographic coordinates). EBMS = Estación Biológica Madre Selva, EBQB = Estación Biológica Quebrada Blanco.

but phenotypically similar taxa, so numerous familiar epithets are now applied more narrowly than before, and unfamiliar names have replaced them in local faunal lists. Additionally, phylogenetic analyses have resulted in several changes in generic usage (especially in the family Phyllostomidae), and the subfamilial nomenclature of phyllostomids has been radically transformed (Baker et al., 2016; Cirranello et al., 2016).

The taxonomic accounts in this monograph explain such nomenclatural issues and summarize phenotypic data that we obtained in the process of documenting species identifications.[1] As in previous faunal monographs, we also compile natural history information associated with collected specimens, although some of this information has already been published (Voss et al., 2016). Matses knowledge about bats was discussed by Fleck et al. (2002), but we summarize additional ethnographic observations in a section that follows the taxonomic accounts. Lastly, we address biogeographic and ecological topics in a concluding discussion.

[1] New bat species discovered in the course of our inventory have been described elsewhere (Simmons et al., 2002; Lim et al., 2010; Velazco and Patterson, 2019; Velazco et al., 2014, 2017).

MATERIAL AND METHODS

Bat Inventory Sites and Capture Methods

Most of our information about bat diversity in the Yavarí-Ucayali interfluve comes from two localities, Jenaro Herrera and Nuevo San Juan, where sustained, multiyear collecting efforts have resulted in long species lists. A brief account of the chronology of sampling efforts and the methods used at these sites and others in our region is important for assessing inventory completeness and inter-site faunal differences.

Jenaro Herrera: Bat inventory efforts at the Centro de Investigaciones Jenaro Herrera from 1988 to 1991 were undertaken to support a study of seed dispersal (Gorchov et al., 1993). The methods employed (documented by Ascorra et al., 1993) consisted almost exclusively of mistnetting, although a few bat roosts were also discovered during this period. The mistnetting activities at Jenaro Herrera from 1988 to 1991 used approximately equal numbers of ground-level nets (operated 0–3 m above the ground) and elevated nets that were raised 5–20 m above the ground. Most netting sessions were 1–3 nights long and were conducted from 18:00 to 24:00 hours, with nets checked for captured bats at 30 minute intervals. Local habitats sampled by mistnetting surveys included clear-cut strips in early stages of regrowth (34 netting sessions), primary forest (18 sessions), secondary forest (7 sessions), and clearings (6 sessions). In total, 2489 mistnet captures of bats were recorded in the course of this three-year project.

Bats were subsequently captured at Jenaro Herrera during a field course organized by the Centro de Ecología y Biodiversidad (CEBIO) from 16 to 24 January 2012, when student participants used ground-level mistnets, elevated mistnets, and harp traps to gain experience with these methods; a few course faculty (including P.M.V.) and R.S.V. also captured bats by mistnetting and searching for roosts for several days after the course ended. Altogether, over 500 bat captures were recorded at Jenaro Herrera during and immediately after the 2012 CEBIO course.[2] Although several roosts were discovered in 2012, most roost inhabitants were left unmolested by course participants and only a few captures were made at roosts during postcourse inventory work (Velazco et al., 2014).

Nuevo San Juan: From 19 May to 11 July 1998, R.S.V. sampled the bat fauna within a 3 km radius of this Matses Indian village by ground-level mistnetting and by searching for roosts using protocols previously described by Simmons and Voss (1998). Mistnetting was conducted on a total of 21 nights during this period, using an average of 3.4 nets per night; nets were moved after each night's session so that no site was netted for more than one consecutive night. Local habitats sampled by mistnetting near Nuevo San Juan included well-drained primary forest (netted for 11 nights), clearings (3 nights), secondary growth (2 nights), *collpas* (swampy mineral licks; 2 nights), river beaches or sandbars (2 nights), and an *aguajal* (palm swamp dominated by *aguaje* palms, *Mauritia flexuosa*; 1 night). Nets were opened just before dark (usually when it was still light enough to read; before 18:00 hr) and were tended continuously until they were closed (always before midnight). A total of 371 mistnet captures of bats were recorded during this period.

Bat roosts in the vicinity of Nuevo San Juan were located with and without the involvement of Matses volunteer helpers in 1998, but R.S.V. collected all specimens (usually by shooting) and recorded data (roost location, habitat, etc.) himself. During a subsequent field season, from 2 September to 12 November 1999, five Matses men were paid salaries to look for bat roosts, with two to four men so employed on any given day. For the first month of the 1999 field season, the Matses did not collect bats or record data themselves but returned to the village to lead D.W.F. to the roosts, where he shot specimens and took notes. Subsequently, Matses assistants

[2] Records from the CEBIO course and from subsequent mistnetting are incomplete, so an exact count of bat captures at Jenaro Herrera in 2012 is unavailable.

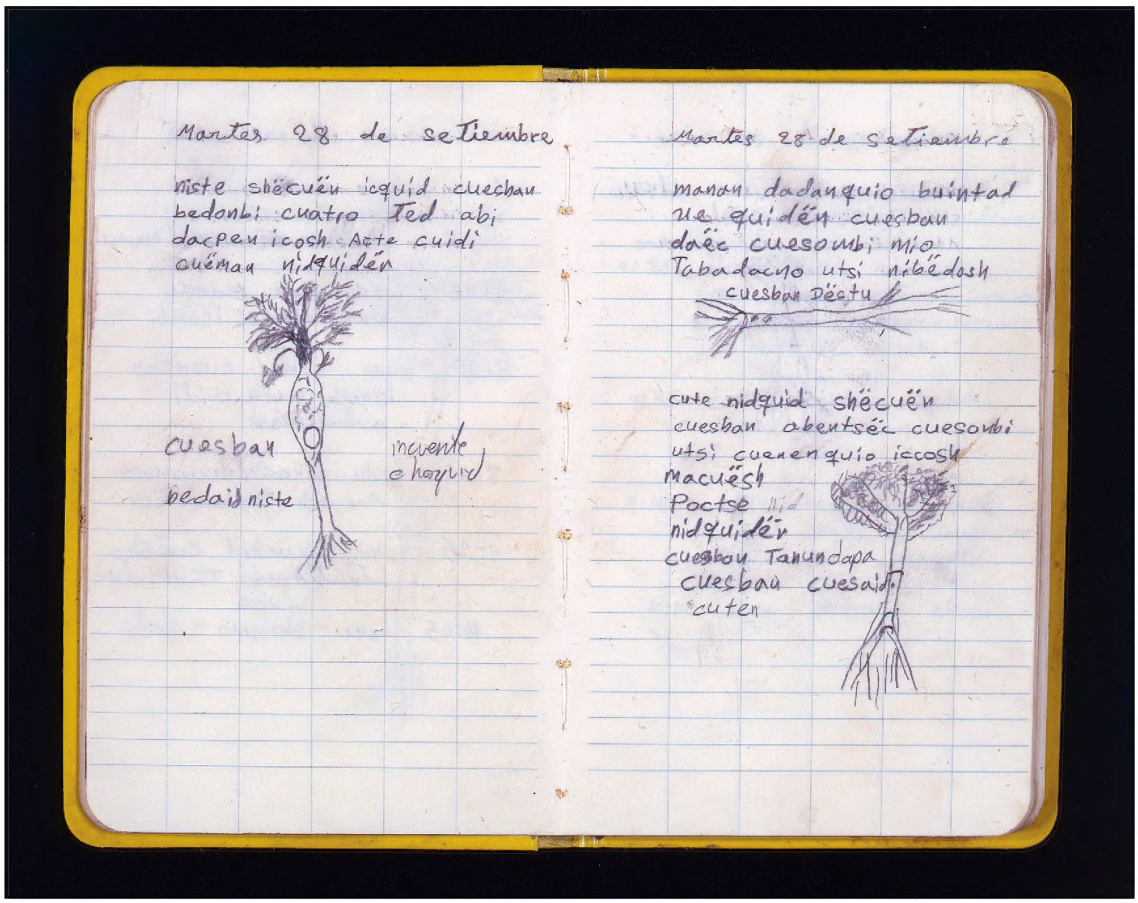


FIG. 3. Two pages from the field notebook of a Matses hunter employed to search for bat roosts near Nuevo San Juan in 1999. The left-hand page, which records the details of the first roost he discovered on September 28th reads as follows (English translation in square brackets): Niste shëcuën icquid cuesban bedombi, cuatro ted. [I got bats that were in an *Iriartea deltoidea* palm cavity, four of them.] Abi dadpen iccosh. [There were still many (i.e., there were many in the roost that were not caught).] Acte cuëman nidquidën. [In one that was standing at the bank of a stream (i.e., the palm tree was growing next to a stream).] Cuesban bedaid niste. [The *I. deltoidea* palm in which the bats were caught (a caption describing the drawing).] Incuente choquid. [Ones that have tails. (Roost-hunters were asked to write down a brief description of bat specimens in case notebook entries and the numbered bags in which collected bats were carried back to the village got mixed up).] The four bats extracted from this roost were all *Molossus rufus*. The swollen trunks of niste palms (*Iriartea deltoiodea*) are often drilled and hollowed out by woodpeckers, and the resulting cavities are later occupied by other species, including bats, toucans, and parrots.

collected specimens and recorded data themselves, and then brought the specimens to D.W.F., who identified, cataloged, and preserved them. Matses collectors recorded their observations in field notebooks (fig. 3), which D.W.F. later translated and transcribed. In total, bats were captured and positively identified from 169 roosts near Nuevo San Juan, of which 115 (68%) were in primary upland forest, 24 (14%) were in secondary vegetation, 22 (13%) were in floodplain (seasonally inundated) forest, 3 (2%) were in *aguajales*, and 3 (2%) were in trees partially submerged in a river (habitat information was not recorded for two roosts).

Other localities: A third locus of bat-collecting activity in our region was centered at the confluence of the Río Tahuayo with the Quebrada Blanco (a right-bank affluent; fig. 2, inset). Cesar Ascorra collected on the lower Quebrada Blanco (at or near the Estación Biológica Quebrada Blanco; see appendix 1) from 23 October to 7 November 1992, when he deployed ground-level and canopy mistnets to sample the fauna of primary forest and secondary vegetation on 13 nights, using methods similar to those described above for his previous fieldwork at Jenaro Herrera (Wilson et al., 1996). Twenty-six years later, from 16 to 22 February 2019, N.B.S. and a team of researchers (including A. Brown, M. Brown, J. Carrera, M. Dunbar, M.B. Fenton, S. Fenton, M. Ingala, D. Johnston, A. Morales, and D. Morningstar) collected bats at three other localities in this area (see appendix 1 for coordinates): (1) El Chino Village, a community of about 60 families living in houses surrounding an open plaza on the right (east) bank of the lower Río Tahuayo; (2) Tahuayo Farm, an abandoned palm plantation overgrown with secondary vegetation on high ground adjacent to the right bank of the lower Quebrada Blanco; and (3) a primary-forest site known as Frog Valley located about one hour upstream from El Chino Village on the Quebrada Blanco. These localities were visited at a time of high water, so all collecting was done on dry land adjacent to flooded habitats. Bats were collected at El Chino Village on three nights with ground-level mistnets set in the plaza and gardens around the village, with a "macro" net (ca. 9 × 30 m) set on the edge of the plaza parallel to the river, and with two "Austbat" (Faunatech-Austbat) harp traps placed in flyways around buildings; bats were also collected by hand from the thatched roof of an open-sided building in the center of the plaza and with hand nets inside other buildings during daylight hours. The Tahuayo Farm locality was sampled for one night with ground-level mistnets and harp traps placed across trails. The Frog Valley locality was sampled for one night with ground-level mistnets and harp traps placed along and across trails, but the field crew returned here on another night to capture bats at a roost. At all these localities mistnets were opened just before dark (ca. 18:30 hr) and were tended continuously until they were closed before midnight. Harp traps were left in place overnight and checked regularly until netting ended, and then checked again at dawn.

Bats were also collected, usually briefly, at 24 other sites in our region as described in appendix 1 and references cited therein.

Taxonomic Methods

Specimens: The morphological specimens we examined and others mentioned below are preserved in the following collections: AMNH (American Museum of Natural History, New York), CEBIOMAS (Centro de Ecología y Biodiversidad, Lima), FMNH (Field Museum, Chicago), LSUMZ (Louisiana State University Museum of Natural Science, Baton Rouge), MPEG (Museu Paraense Emílio Goeldi, Belém), MUSA (Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa, Arequipa), MUSM (Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima), MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo), and ROM (Royal Ontario Museum, Toronto).

Measurements: All measurements of bats reported below were taken from adult individuals with closed epiphyses. Standard external measurements (total length, length of tail, hindfoot length, ear length) were transcribed from specimen labels or other records made by the collectors, whereas forearm length and craniodental measurements were taken from preserved voucher specimens using digital calipers and recorded to the nearest 0.01 mm. Linear measurements are given in millimeters (mm); body mass is reported in grams (g). Descriptive statistics (mean and observed range) were cal-

culated for all samples. Measurements are defined as follows:

ToL (total length): distance from the tip of the snout to the tip of the last caudal vertebra

LT (length of tail): measured from the point of dorsal flexure of the tail with the sacrum to the tip of the last caudal vertebra

HF (hindfoot length): distance from the anterior edge of the base of the calcar to the tip of the claw of the longest toe

E (ear length): distance from the basal notch to the fleshy tip of the pinna

F (forearm length): distance from the elbow (tip of the olecranon process) to the distal end of the wrist (including the carpals) when the wing is partially or fully folded

GLS (greatest length of skull): distance from the posteriormost point on the occiput to the anteriormost point on the premaxilla

CIL (condyloincisive length): distance from the posteriormost point on the occipital condyles to the anteriormost point on the upper incisors

CCL (condylocanine length): distance from the posteriormost point on the occipital condyles to the anteriormost point on the upper canines

PB (postorbital breadth): least breadth across the frontals posterior to the postorbital processes or bulges

ZB (zygomatic breadth): greatest transverse dimension across the zygomatic arches

BB (braincase breadth): greatest breadth of the globular part of the braincase

MB (mastoid breadth): greatest cranial breadth across the mastoid region

MTL (maxillary toothrow length): distance from the anteriormost edge of the canine crown to the posteriormost edge of the crown of the last molar

BAM (breadth across molars): greatest breadth between the outer edges of the crowns of the right and left upper molars

BAC (breadth across canines): greatest breadth between the outer edges of the crowns of the right and left upper canines.

Ethnographic and Linguistic Methods

Matses knowledge about bats and the terminology that the Matses use to talk about bats were the topics of a previous report that was based on ethnobiological interviews, elicitation of bat names using freshly captured specimens, and recordings of short monologs. The relevant methods have already been described in detail (Fleck et al., 2002), so only a brief summary is needed here. During the initial interviews (conducted in 1994), five Matses hunters from several villages were asked to list all the kinds of bats they knew. Because D.W.F. was not fluent in Matses at the time, these interviews were conducted in Spanish. Interviewees were prompted once ("¿Cuantas calidades de kuesban[3] hay?"), and they were allowed to give as many responses as they wished without interruption or further prompting. Later (from May to July of 1998), misnetting at Nuevo San Juan provided an ample supply of freshly killed bats that D.W.F. used to elicit bat names from Matses informants. Dead bats were presented to informants on a tray (including multiple individuals of most species, each tagged with an identification number); informants were asked, sometimes one person at a time but sometimes in groups, to name the bats, which they were encouraged to handle and examine closely. During the same (1998) field season, monologs about the natural history of local mammals were elicited from seven men and recorded on digital minidisk; all monologs were in the Matses language. To elicit these texts, interviewees were asked to talk about a single named terminal folk taxon (folk species; e.g., kuesban) and were not interrupted or asked to continue once they had stopped. During a subsequent field season (in 1999), D.W.F. also recorded Matses bat names while accompanying hunters who were hired to search for bat roosts near Nuevo San Juan; bat names were elicited at the roost site as the Matses examined the shot bats.

More recently (in December 2010), additional monologs about bat natural history were col-

[3] Kuesban is the only lexicalized term for "bat" in the Matses language. In the traditional orthographic system followed by Fleck et al. (2002), this word was spelled cuesban.

lected from two Matses men at Estirón (a village on the Quebrada Chobayacu about 40 km SE of Nuevo San Juan). Prior to recording each monolog, each man was asked to list all of the kinds of bats with which he was familiar. This listing exercise differed from those carried out in 1994 because it was followed up by discussing elicited descriptive terms with the narrators to reduce redundancy and ambiguity, such that multiple terms used to refer to a single type of bat (e.g., "big bats," "ones having long wings") were avoided. Then, D.W.F. prompted the interviewees by asking them to talk about each unique type of bat thus identified using only the most specific descriptor (e.g., "bat that lives in termite nests"). These recordings were transcribed and translated into Spanish by bilingual Matses assistants, whose work D.W.F. subsequently checked for accuracy (consulting the narrators when it was not clear what was meant) and translated into English; linguistic, biological, and other commentary were added before the recordings and their transcripts were deposited with the Endangered Languages Archive at the School of Oriental and African Studies, University of London (https://www.soas.ac.uk/elar/).

SYSTEMATIC ACCOUNTS

The family-level classification in these accounts follows Simmons (2005), but the subfamily classification of phyllostomids follows the revised system of Cirranello et al. (2016). Under headings for families, subfamilies, and genera we summarize information about distribution, diversity, diagnostic morphological traits, and numbers of subordinate taxa known to be present in the Yavarí-Ucayali interfluve. Subheadings in our species accounts summarize information about the voucher material we examined and about unvouchered observations (numbers of individuals recorded acoustically, observed but not captured, or captured and released). Additionally (under Identification), we explain the criteria we used to establish taxonomic identifications and note any recent changes in nomenclature that affect binomial usage. Natural history information is summarized under Remarks; most observations summarized under this heading and in accompanying tables use roost descriptors (e.g., "animal burrow," "cavity in standing tree") previously defined by Voss et al. (2016). All proper names for collection localities in our region are defined and georeferenced in appendix 1.

Family Emballonuridae Gervais, 1856

The pantropical family Emballonuridae (commonly known as sheath-tailed or sac-winged bats) includes 55 currently recognized Recent species in 14 genera, of which 22 species in 8 genera are Neotropical (Simmons, 2005; Simmons and Cirranello, 2020). These rather delicate bats are characterized externally by long, soft fur; lack of facial ornamentation; relatively large eyes; and presence of a broad uropatagium, from which the tip of the tail emerges dorsally about halfway along the length of the membrane (Emmons and Feer, 1997; Simmons and Voss, 1998; Hood and Gardner, 2008; Reid, 2009; López-Baucells et al., 2018). Most Neotropical emballonurids have glandular wing sacs located in the propatagium near the elbow (Emmons and Feer, 1997; Reid, 2009; López-Baucells et al., 2018). Hood and Gardner (2008) provided a key to the genera and species of South American emballonurids based on external and craniodental characters. Eleven species in six genera are known from the Yavarí-Ucayali interfluve. Published records from localities adjacent to the Yavarí-Ucayali interfluve include another two emballonurid species that might also occur in our study area (appendix 2).

Cormura brevirostris (Wagner, 1843)

VOUCHER MATERIAL (TOTAL = 29): Jenaro Herrera (MUSM 5815), Nuevo San Juan (AMNH 272786, 272817, 272838, 272839, 273036, 273037, 273067, 273070, 273108, 273109, 273132; MUSM 13197–13199, 13200, 15174–15178, 15248),

TABLE 1

External and Craniodental Measurements (mm) and Weights (g) of *Cormura*, *Cyttarops*, and *Diclidurus* from the Yavarí-Ucayali Interfluve

	Cormura brevirostris		*Cyttarops alecto*	*Diclidurus isabella*
	Males[a]	Females[b]	MUSA 15288 ♂	MUSM 37068 ♀
W	8.5 (7.0–10.4) 8	9.1 (5.8–11.5) 14	5.6	—
ToL	67.6 (62–74) 9	69.6 (62–77) 16	75	—
LT	13.9 (12–16) 9	14.1 (12–17) 16	23	13
HF	7.9 (7–8) 9	8.2 (7–9) 16	10	11
E	14.4 (12–16) 8	14.8 (13–17) 13	13	15
F	46.3 (45.0–49.0) 7	47.3 (44.0–49.0) 15	44.4	58.8
CCL	14.3 (14.0–14.4) 4	14.2 (13.6–14.7) 4	12.6	16.7
ZB	9.9 (9.7–10.0) 3	10.0 (9.8–10.1) 4	8.9	11.9
MTL	6.4 (6.3–6.4) 4	6.3 (5.9–6.6) 7	5.4	7.5
BAM	7.3 (7.2–7.3) 4	7.2 (6.8–7.3) 6	6.1	8.2

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74103, 272838, 272839, 273036, 273070; FMNH 89124; MUSM 13198, 15175, 15178, 15248.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74104, 74106, 272786, 272817, 273037, 273067, 273108, 273109, 273132; FMNH 89122, 89123; MUSM 5815, 13197, 13199, 13200, 15174, 15176, 15177.

Orosa (AMNH 74103, 74104, 74106), Quebrada Esperanza (FMNH 89122–89124), Río Blanco (MUSA 15102); see table 1 for measurements.

Unvouchered observations: *Cormura brevirostris* was recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Cormura brevirostris* can be easily distinguished from other emballonurids by the form of the wing sac, which is large (extending from near the elbow to almost the edge of the propatagium) and opens laterally toward the wing tip (for illustrations see Sanborn, 1937; Bernard, 2003; Reid, 2009; and López-Baucells et al., 2018). Another diagnostic character is the attachment of the wings to the metatarsals near the base of the toes; other brownish emballonurids with wing sacs have wings that attach at the ankle, not on the foot (Sanborn, 1937; Reid, 2009; López-Baucells et al., 2018). On some study skins the aforementioned characters may be difficult to evaluate, with the result that skins of *Cormura* can be confused with those of *Peropteryx*. One useful craniodental character for distinguishing these externally similar genera is the shape of the first upper premolar, which is tricuspidate in *Cormura* but is a unicuspid spicule in *Peropteryx* (Hood and Gardner, 2008). Craniodental characters and measurements of *C. brevirostris* from northern Peru and elsewhere were provided by Sanborn (1937), Husson (1962, 1978), Ceballos-Bendezú (1968), and Simmons and Voss (1998). No subspecies of *Cormura brevirostris* are currently recognized (Hood and Gardner, 2008).

Sanborn (1937), Ceballos-Bendezú (1968), Fleck et al. (2002), and Medina et al. (2015) correctly identified their specimens of *Cormura brevirostris* from Orosa, Quebrada Esperanza, Nuevo San Juan, and Río Blanco, respectively, but Ascorra et al. (1993) misidentified the specimens from Jenaro Herrera as *Peropteryx kappleri*. Sanborn (1937) described two color phases in *Cormura*, one deep blackish brown and the other reddish brown. The reddish-brown phase is characteristic of specimens from the Yavarí-Ucayali interfluve, which are morphologically indistinguishable from the mate-

TABLE 2

Roosting Groups of *Cormura brevirostris* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
28 Jun 1998	under fallen tree	unknown	unknown	1 ad. male, 2 ad. females
4 Jul 1998	under fallen tree	3 or 4	no	1 ad. male, 1 ad. female
2 Sep 1999	under fallen tree	3	no	1 ad. male, 1 ad. female
8 Sep 1999	exposed on standing tree	2	yes	1 ad. male, 1 ad. female
9 Sep 1999	under fallen tree	3	no	1 ad. male
22 Sep 1999	under fallen tree	3	no	1 ad. female
22 Sep 1999	under fallen tree	2	no	1 ad. female
6 Oct 1999	under fallen tree	3	yes	1 ad. male, 2 ad. females
22 Oct 1999	under fallen tree	2	yes	1 ad. male, 1 ad. female
22 Oct 1999	under fallen tree	1	yes	1 ad. female
3 Nov 1999	under fallen tree	2	no	1 ad. male

rial we examined from French Guiana (Simmons and Voss, 1998), Brazil (e.g., AMNH 78801), Ecuador (e.g., AMNH 68039), Panama (e.g., AMNH 123996), and Venezuela (e.g., AMNH 130726).

Remarks: The only definite ecological information about this species in our region is from Nuevo San Juan, where we took three individuals in ground-level mistnets in a swampy mineral lick (*collpa*) and 21 others at roosts. We found 11 roosts of *Cormura brevirostris* near Nuevo San Juan, usually at or near ground level on the underside of fallen trees (table 2); one group, however, occupied a shallow concavity between the buttresses of a standing tree about 4 m above the ground. All roosts were in primary forest, often on hilltops or hillsides, but also in ravines, valley bottoms, and a palm swamp; three roosts were found under trees that had fallen across small streams. *Cormura brevirostris* was not found roosting with any other bat species.

The roosting habits of *Cormura brevirostris* near Nuevo San Juan are consistent with the behavior of this species throughout Amazonia, where most reported roosts have been found under or inside fallen trees (e.g., by Brosset and Charles-Dominique, 1990; Simmons and Voss, 1998).

Cyttarops alecto Thomas, 1913

Voucher material (total = 1): Quebrada Sábalo (MUSA 15288); see table 1 for measurements.

Unvouchered observations: See Remarks.

Identification: *Cyttarops* is a monotypic genus that is easily distinguished from other emballonurids by its long, silky, smoky-gray to blackish pelage; a uropatagium bearing neither specialized sacs nor glands; a long, narrow postorbital process that is not fused to the supraorbital ridge; and by the absence of a gap between the two upper premolars (Jones and Hood, 1993; Hood and Gardner, 2008; López-Baucells et al., 2018). Descriptions and measurements of *C. alecto* were provided by Starrett and Casebeer (1968), Jones and Hood (1993), Hood and Gardner (2008), Velazco et al. (2011), Tavares et al. (2012), and Ludeña and Medina (2017). No subspecies are currently recognized (Hood and Gardner, 2008).

Medina et al. (2015) erroneously reported the adult male specimen from Quebrada Sábalo as *Centronycteris maximiliani* based on external characters. Subsequent study of craniodental morphology and re-examination of the skin resulted in the correct identification (Ludeña and Medina, 2017).

Remarks: The Quebrada Sábalo specimen was captured in a mistnet suspended 22 m above ground (Medina et al., 2015). Several individuals of a small grayish bat that D.W.F. and his Matses companions flushed from the fronds of a *Mauritia flexuosa* palm in a palm swamp (*aguajal*) at Nuevo San Juan in 1999 may have belonged to this species.

Genus *Diclidurus* Wied-Neuwied, 1820

The genus *Diclidurus* currently includes four species that range from Mexico to Paraguay (Simmons, 2005; Simmons and Cirranello, 2020). Members of this genus are not easily captured because they are rapid fliers active above the canopy or in open areas over water, where they are hard to capture with standard mistnetting techniques (Kalko et al., 1996; Lim et al., 1999; Ochoa-G. et al., 2008). Accordingly, most knowledge of these bats has been gained through use of shotguns, aerial nets, acoustic monitoring, and/or searching for roosts.

Species of *Diclidurus* are characterized by distinctively whitish (sometimes entirely white) or very pale coloration. Hood and Gardner (2008) provided a key based on external and cranial characters, and López-Baucells et al. (2018) provided a key based on external characters alone (but see comments under *D. isabella*, below). During the 2012 CEBIO bat course, two acoustic forms of *Diclidurus* were detected (possibly *D. albus* and *D. scutatus*) but only one species (*D. isabella*) has been positively identified from voucher material collected in the Yavarí-Ucayali interfluve.

Diclidurus isabella (Thomas, 1920)

Figure 4A

Voucher material (total = 1): Lago Preto (MUSM 37068); see table 1 for measurements.

Unvouchered observations: None.

Identification: Thomas (1920), Hood and Gardner (2008), and Garbino et al. (2013) described external and craniodental characteristics of *Diclidurus isabella*. Although López-Baucells et al. (2018) suggested that this species can be distinguished from other congeners based on color and forearm measurements alone, our experience suggests that unambiguous identification of *Diclidurus* species requires examination of craniodental features. *Diclidurus isabella*, in particular, can be identified by its pale-brownish fur, presence of an evenly concave posterior border of the palate, and a mesopterygoid fossa that reaches the level of the anterior cusps on M3 (Hood and Gardner, 2008). Craniodental characters and measurement of *D. isabella* were also discussed by Thomas (1920), Lim et al. (1999), Ochoa-G. et al. (2008), and Garbino et al. (2013). No subspecies of *D. isabella* are currently recognized (Hood and Gardner, 2008).

Escobedo and Velazco (2012) misidentified the adult female (fig. 4A) from Lago Preto as *Diclidurus scutatus* based on external characters, but subsequent examination of the skull resulted in the current identification. This specimen represents the first record of *D. isabella* for Peru.

Remarks: The Lago Preto specimen was captured at 19:30 hr on a night with a full moon in a mistnet suspended 10 m above ground next to the Río Yavarí; the capture habitat was riparian forest with an open understory.

Genus *Peropteryx* Peters, 1867

The genus *Peropteryx* includes five species that are widely distributed across the Neotropics (Lim et al., 2010; Simmons and Cirranello, 2020). Species of *Peropteryx* are distinguished from members of other emballonurid genera by having a naked (unfurred) face, a wing attachment at the ankle, and a poorly developed wing sac located near the leading edge of the membrane. Lim et al. (2010) summarized morphological characters and measurements that are useful for distinguishing species of *Peropteryx*, of which they reported three from the Yavarí-Ucayali interfluve: *P. kappleri*, *P. leucoptera*, and *P. pallidoptera*. All three

FIG. 4. Photographs of **A,** an adult female (MUSM 37068) *Diclidurus isabella* captured at Lago Preto; **B**, an adult female *Peropteryx leucoptera* captured at Tahuayo Farm; and **C**, an adult *P. macrotis* captured at Frog Valley. Photographs by Mark Bowler (A) and Brock Fenton (B, C).

TABLE 3

External and Craniodental Measurements (mm) and Weights (g) of *Peropteryx kappleri* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	8.3 (8.0–8.7) 4	9.5 (6.8–11.4) 5
ToL	72.0 (70–76) 4	74.4 (65–82) 5
LT	14.5 (13–17) 4	14.8 (11–17) 5
HF	10.8 (8–12) 4	11.2 (11–12) 5
E	17.7 (17–19) 3	17.2 (15–19) 5
F	49.6 (48.0–50.5) 4	51.8 (47.0–54.0) 5
CCL	15.5 (15.4–15.5) 2	15.5 (15.4–15.6) 2
ZB	10.4 (10.4–10.4) 2	10.5 (10.4–10.6) 2
MTL	7.4 (7.3–7.4) 2	7.4 (7.1–7.6) 2
BAM	8.0 (7.8–8.1) 2	7.8 (7.7–7.9) 2

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272797, 272799; MUSM 6976, 15245.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272798, 273086, 273174; MUSM 13225, 15244.

species occur sympatrically at Nuevo San Juan, and a fourth (*P. macrotis*) has subsequently been captured elsewhere in our region.

Peropteryx kappleri Peters, 1867

Voucher material (total = 9): Jenaro Herrera (MUSM 6976), Nuevo San Juan (AMNH 272797–272799, 273086, 273174; MUSM 13225, 15244, 15245); see table 3 for measurements.

Unvouchered observations: None.

Identification: *Peropteryx kappleri* is easily distinguished from other members of the genus by its large size (forearm >46.5 mm), uniformly brown wings, absence of a transverse band of skin connecting the ears, a skull with a relatively narrow but dorsally inflated rostrum, small and shallow lateral pterygoid pits separated by the basisphenoid pit, and presence of a posterior cusp on the anterior upper premolar (Lim et al., 2010). Descriptions and measurements of *P. kappleri* were provided by Sanborn (1937), Goodwin and Greenhall (1961), Husson (1962, 1978), Jones and Hood (1993), Simmons and Voss (1998), Lim et al. (2010), McDonough et al. (2010), and Velazco and Patterson (2019). Two subspecies are currently recognized: *P. k. kappleri* (Central America to Ecuador, Venezuela, the Guianas, and southeastern Brazil) and *P. k. intermedius* (southern Peru) (Hood and Gardner, 2008).

Fleck et al. (2002) and Lim et al. (2010) correctly identified our material from Nuevo San Juan as *Peropteryx kappleri*. The specimen from Jenaro Herrera is morphologically indistinguishable from the Nuevo San Juan material, exhibiting all the diagnostic characters for this species as described by Lim et al. (2010) and noted above. All examined specimens from the Yavarí-Ucayali interfluve are morphologically indistinguishable from French Guianan material reported by Simmons and Voss (1998).

Remarks: The only definite ecological information about *Peropteryx kappleri* in our region is from Nuevo San Juan, where we found five roosts of this species, all of them inside hollow logs or on the undersides of fallen trees (table 4). Four roosts were in well-drained primary forest on hilltops or hillsides, but one was in secondary growth from an old blowdown. *Peropteryx kappleri* was not found roosting with any other bat

TABLE 4

Roosting Groups of *Peropteryx kappleri* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
25 Jun 1998	inside hollow log	5	no	2 ad. males, 2 ad. females
11 Sep 1999	inside hollow log	4	no	1 ad. male, 2 ad. females
23 Oct 1999	inside hollow log	2	no	1 ad. female
23 Oct 1999	under fallen tree	3	no	1 juvenile
26 Oct 1999	under fallen tree	1	yes	1 ad. male

species. Although this species was also captured at Jenaro Herrera, the circumstances of capture there are unknown.

Our roost observations are consistent with previous reports that, in the absence of rocks and caves, *Peropteryx kappleri* usually roosts under or inside fallen trees (Bradbury and Vehrencamp, 1976; LaVal, 1977; Simmons and Voss, 1998).

Peropteryx leucoptera Peters, 1867

Figures 4B, 5A

Voucher material (total = 3): Nuevo San Juan (AMNH 273182, 273197; MUSM 15247); see table 5 for measurements.

Unvouchered observations: A single individual of *Peropteryx leucoptera* was captured at Tahuayo Farm on 19 February 2019.

Identification: *Peropteryx leucoptera* is distinguished from other congeners by its intermediate size (forearm 42–46 mm), translucent wings that gradually darken to brown near the body, presence of a transverse band of skin connecting the ears, a skull with a relatively broad rostrum that is not dorsally inflated, large and deep lateral pterygoid pits separated by the presphenoid[4] and the basisphenoid pit, and presence of a peglike anterior upper premolar (fig. 5A; Lim et al., 2010). Descriptions and measurements of *P. leucoptera* were provided by Sanborn (1937), Husson (1962, 1978), Jones and Hood (1993), Simmons and Voss (1998), Lim et al. (2010), and McDonough et al. (2010). Two subspecies are currently recognized: *P. l. leucoptera* (southeastern Colombia and Ecuador, northeastern Peru, northern Brazil, southern Venezuela, and the Guianas) and *P. l. cyclops* (southeastern Peru) (Hood and Gardner, 2008; Lim et al., 2010; McDonough et al., 2010).

Fleck et al. (2002) and Lim et al. (2010) correctly identified their material from Nuevo San Juan as *Peropteryx leucoptera*. The Nuevo San Juan specimens are slightly larger in most measurements than those reported from the Guianas, and they are slightly smaller in some measurements that those of the holotype of *P. l. cyclops* (Lim et al. 2010: table 1), but after careful morphological comparison of the specimens from Nuevo San Juan with material from other localities throughout the distribution of the species, we found no morphological support for the continued recognition of *P. l. cyclops* as a distinct subspecies.

Remarks: Ascorra et al. (1993) reported a roosting group of this species that was found under a dead palm frond in a swamp at Jenaro Herrera, but no voucher material was collected, and we consider the identification to be problematic. The individual from Tahuayo Farm was captured in a ground-level mistnet in secondary vegetation, but all the other individuals of *Peropteryx leucoptera* from our region were taken from roosts at Nuevo San Juan: (1) one group of two individuals was found on 26 October 1999 perched on the underside of a fallen tree next to a stream in primary forest (one adult male was collected); (2) another pair was found inside a hol-

[4] Lim et al. (2010) mistakenly identified the bone that separates the pterygoid pits in *Peropteryx leucoptera* and *P. pallidoptera* as a "mesopterygoid extension." However, the bone that separates the pterygoid pits is the caudal portion of the presphenoid (fig. 5).

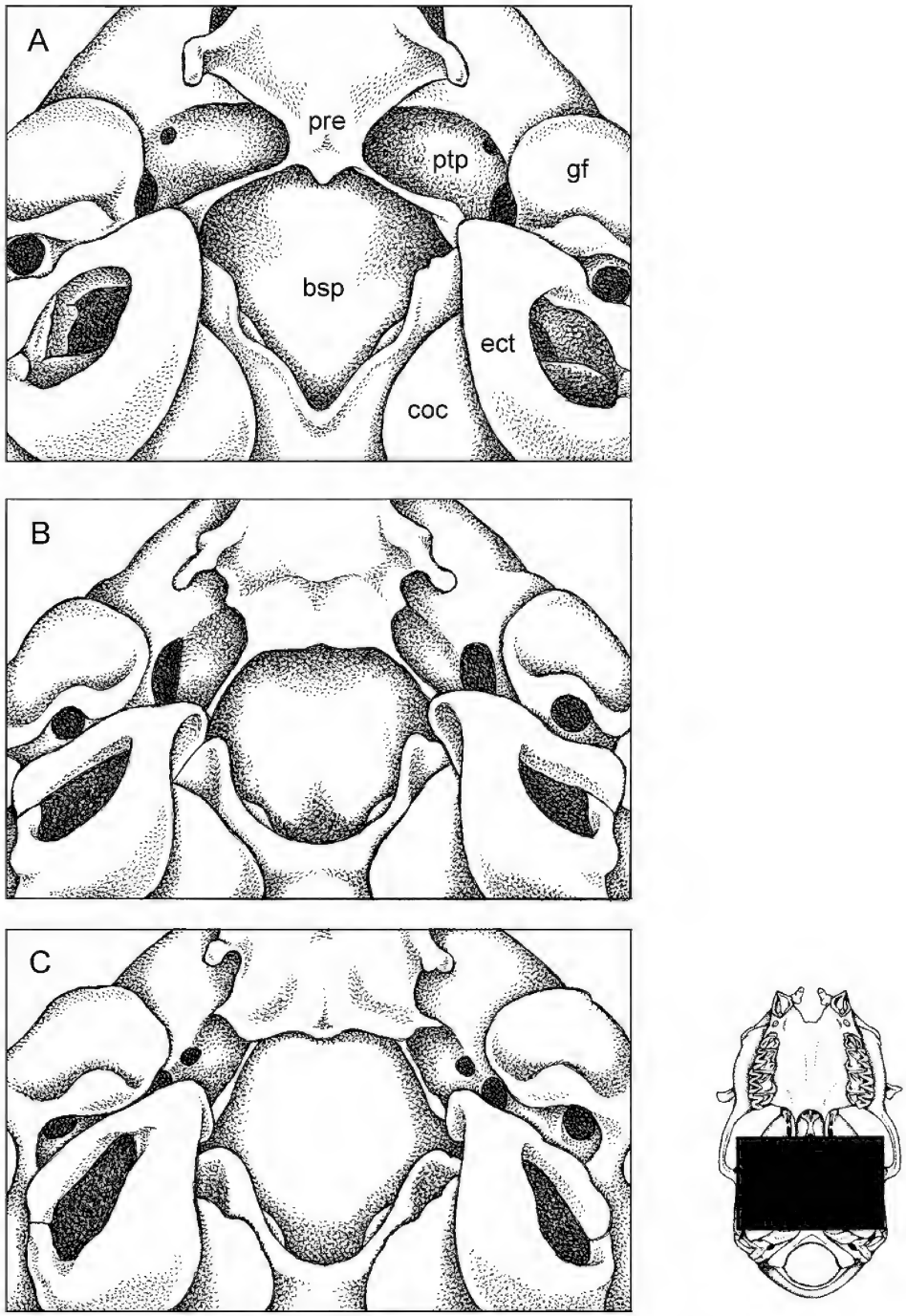


FIG. 5. Basicranial views of *Peropteryx leucoptera* (**A**, AMNH 273182), *P. pallidoptera* (**B**, MUSM 13228), and *P. macrotis* (**C**, AMNH 266005) illustrating taxonomic differences in the size and separation of the pterygoid pits. In *P. leucoptera*, large pterygoid pits (**ptp**) are separated by the presphenoid (**pre**) and the basisphenoid pit (**bsp**). In *P. pallidoptera*, small pterygoid pits are separated by the presphenoid and the basisphenoid pit. In *P. macrotis*, small pterygoid pits are separated only by the basisphenoid pit. Other abbreviations: **coc**, cochlea; **ect**, ectotympanic; **gf**, glenoid fossa.

TABLE 5

External and Craniodental Measurements (mm) and Weights (g) of *Peropteryx leucoptera* and *P. pallidoptera* from the Yavarí-Ucayali Interfluve

	P. leucoptera	*P. pallidoptera*	
	Males[a]	Males[b]	Females[c]
W	8.2 (8.0–8.5) 3	6.4 (4.3–8.5) 2	5.5 (4.1–7.6) 15
ToL	70.3 (66–76) 3	63.7 (60–69) 3	62.8 (58–67) 16
LT	15.0 (13–16) 3	11.3 (10–13) 3	12.5 (10–14) 17
HF	10.0 (10–10) 3	9.0 (9–9) 3	9.3 (8–10) 17
E	19.7 (19–20) 3	16.3 (15–19) 3	15.3 (14–17) 17
F	45.3 (45.0–46.0) 3	42.0 (39.0–46.0) 3	41.9 (41.0–43.0) 12
CCL	14.4 (14.3–14.4) 2	12.0 (11.9–12.2) 2	12.1 (11.7–12.3) 10
ZB	10.0 (9.8–10.2) 2	8.0 (7.8–8.2) 2	8.2 (8.0–8.6) 11
MTL	6.4 (6.4–6.5) 2	5.3 (5.3–5.4) 3	5.4 (5.2–5.5) 11
BAM	7.4 (7.3–7.5) 2	5.9 (5.8–5.9) 3	6.1 (5.7–6.4) 11

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273182, 273197; MUSM 15247.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74107; FMNH 89104; MUSM 13226, 15251.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272671, 272726, 272827, 272854, 272855, 273042, 273116, 273185; FMNH 89103; MUSM 13227–132230, 15246, 15249–15250, 15252.

low log in hilltop primary forest on 3 November 1999 (one adult male was collected); and (3) a group of three individuals was found on the underside of a fallen tree in primary upland forest near a stream on 12 November 1999 (one adult male was collected). *Peropteryx leucoptera* was not found roosting with any other bat species.

Our observations from Nuevo San Juan are consistent with those of several previous authors (e.g., Simmons and Voss, 1998; Bernard, 1999; Díaz and Linares García, 2012; Rengifo et al., 2013) who reported that, in rock- and caveless landscapes, *Peropteryx leucoptera* usually roosts inside or under fallen trees.

Peropteryx macrotis (Wagner, 1843)

Figures 4C, 5C

Voucher material: None.

Unvouchered observations: Five individuals of *Peropteryx macrotis* were captured at Frog Valley on 20 February 2019 (see Remarks).

Identification: *Peropteryx macrotis* is distinguished from other members of the genus by its intermediate size (forearm 41–46 mm), uniformly brown wings, presence of a transverse band of skin connecting the ears, a skull with a relatively broad rostrum that is not dorsally inflated, small and shallow lateral pterygoid pits separated by the basisphenoid pit, and presence of an anterior upper premolar with a posterior cusp (fig. 5C; Lim et al., 2010). Descriptions and measurements of *P. macrotis* were provided by Sanborn (1937), Husson (1962, 1978), Jones and Hood (1993), Simmons and Voss (1998), Lim et al. (2010), and McDonough et al. (2010). No subspecies are currently recognized.

Remarks: All the *Peropteryx macrotis* captured at Frog Valley were females that we found roosting together in a large hollow log (approximately 25 m long and perhaps 2 m in diameter) in unflooded primary forest. This roost also contained *Peropteryx pallidoptera*, *Hsunycteris pattoni*, and large

TABLE 6

Roosting Groups of *Peropteryx pallidoptera* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
22 May 1998	under fallen tree	unknown	unknown	1 ad. male, 2 ad. females
11 Jun 1998	inside hollow log	2	no	1 ad. female
30 Jun 1998	undercut earth bank	3	yes	3 ad. females
8 Jul 1998	under fallen tree	2	no	1 ad. female
8 Jul 1998	under fallen tree	2	yes	2 ad. females
4 Sep 1999	animal burrow/hole	unknown	unknown	1 ad. female
16 Sep 1999	unmodified foliage	1	yes	1 ad. female
22 Sep 1999	animal burrow/hole	2	no	1 ad. female
23 Sep 1999	animal burrow/hole	4	no	2 ad. males, 1 ad. female
11 Oct 1999	undercut earth bank	1	yes	1 ad. female
27 Oct 1999	under fallen tree	1	yes	1 ad. female
2 Nov 1999	under fallen tree	1	yes	1 ad. female

numbers of *Carollia brevicauda* and *Trachops cirrhosus*. Both species of *Peropteryx* were roosting near the log entrance, whereas the other species were roosting out of sight in the dark interior.

Peropteryx pallidoptera Lim et al., 2010

Figure 5B

Voucher material (total = 22): Nuevo San Juan (AMNH 272671, 272726, 272827, 272854, 272855, 273042, 273116, 273185; MUSM 13226–13230, 15246, 15249–15252), Orosa (AMNH 74107), Quebrada Esperanza (FMNH 89103, 89104), Quebrada Lobo (MUSA 15134); see table 5 for measurements.

Unvouchered observations: Two individuals were captured at Frog Valley on 20 February 2019.

Identification: *Peropteryx pallidoptera* was recently described based on specimens from three localities, two of which occur in the Yavarí-Ucayali interfluve. This species can be distinguished from other congeners by having transparent but brown-tinged wing membranes; pale-brown arms and manual digits; ears that are not connected by a transverse band of skin; a skull with a narrow rostrum that is not dorsally inflated; and small, shallow pterygoid pits separated by the presphenoid and the basisphenoid pit (fig. 5B; Lim et al. 2010: figs. 1, 2). Descriptions and measurements of *P. pallidoptera* were provided by Lim et al. (2010), McDonough et al. (2010), Castro et al. (2012), and Suárez-Castro et al. (2012). No subspecies are currently recognized in *P. pallidoptera* (Lim et al., 2010).

Specimens of *Peropteryx pallidoptera* from Nuevo San Juan were identified as *P.* cf. *macrotis* by Fleck et al (2002). This material was subsequently included as part of the type series of *P. pallidoptera* by Lim et al. (2010). Medina et al. (2015) correctly identified their specimen from Quebrada Lobo as *P. pallidoptera*.

Remarks: The two individuals captured at Frog Valley, both females, were taken from the same hollow-log roost described in the account for *P. macrotis* (above). All the specimens of *Peropteryx pallidoptera* from Nuevo San Juan were taken from roosts (table 6). Half these roosts were encountered inside or under fallen trees, but undercut earth banks and holes (probably excavated by armadillos) in the sides

TABLE 7

External and Craniodental Measurements (mm) and Weights (g) of *Rhynchonycteris naso* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	3.6 (3.2–4.3) 9	4.5 (3.5–5.2) 5
ToL	57.2 (55–59) 10	60.6 (59–64) 5
LT	13.7 (12–16) 10	15.6 (15–17) 5
HF	7.0 (6–8) 15	7.0 (6–8) 7
E	13.5 (13–15) 10	12.8 (9–15) 4
F	36.2 (34.0–37.5) 14	38.4 (34.7–40.8) 6
CCL	10.4 (10.4–10.4) 2	10.7
ZB	7.0 (7.0–7.1) 2	7.0 (6.8–7.1) 2
MTL	4.5 (4.4–4.5) 2	4.5
BAM	4.6 (4.6–4.7) 2	4.6 (4.5–4.7) 2

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272684, 272835, 272852, 273141, 273175; FMNH 19960, 19962, 19964–19967; MUSM 4355, 13249–13251, 15264–15265.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272685, 273150, 278459; FMNH 19961, 19963; MUSM 13248, 15266.

of stream headwater gullies were also used. Exceptionally, one bat was found beneath the unmodified leaf of a large monocot (probably *Heliconia* sp.). Most (11 of 12) roosts were in well-drained primary forest, often on hilltops or hillsides, but also in valley bottoms; one roost, however, was found in old secondary growth (probably a long-abandoned swidden). *Peropteryx pallidoptera* was usually found roosting alone at Nuevo San Juan, but one roosting group shared a fallen tree with a group of *Saccopteryx bilineata*, and another shared a deep hole in the side of a stream headwater gully with groups of *Micronycteris hirsuta* and *Carollia brevicauda*. The circumstances of capture at other localities in our region are unknown.

Based on available natural history information about this widespread but only recently described species (Lim et al., 2010; Díaz and Linares García, 2012; Suárez-Castro et al., 2012), *Peropteryx pallidoptera* seems to roost in a variety of ground-level refugia, but more roosts have been found under fallen trees than in any other reported situation.

Rhynchonycteris naso Wied-Neuwied, 1820

Figure 6

Voucher material (total = 24): Amelia (FMNH 19960–19967), Isla Padre (MUSM 4355), Jenaro Herrera (AMNH 278459), Nuevo San Juan (AMNH 272684, 272685, 272835, 272852, 273141, 273150, 273175; MUSM 13248–13251, 15264–15266); see table 7 for measurements.

Unvouchered observations: Roosting groups of *Rhynchonycteris naso* were observed at Anguila and Wiswincho during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015). Additionally, four individuals of *R. naso* were captured at Quebrada Buenavista during the Yavarí Rapid Biological Inventory (Escobedo, 2003), and we captured another three individuals at El Chino Village in 2019. *Rhynchonycteris naso* was also identified using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Rhynchonycteris* is a widespread monotypic genus that ranges from Mexico to eastern Brazil (Simmons, 2005; Simmons and

FIG. 6. Photographs of **A,** an adult female (ROM 122161) *Rhynchonycteris naso* captured at Jenaro Herrera; and **B**, a group of three adults *R. naso* roosting under a palm-thatched roof at El Chino Village. Photographs by Burton Lim (A) and Brock Fenton (B).

Cirranello, 2020). *Rhynchonycteris* is easily distinguished from other Neotropical emballonurids by the absence of wing sacs, and by having a long nose that projects well beyond the lower lip, two pale dorsal stripes, frosted dark-brown dorsal fur, a dark-brown face contrasting with much paler ventral fur, and forearms that are sparsely haired but adorned with tufts of whitish fur (Reid, 2009; López-Baucells et al., 2018). The following craniodental characters are also useful for diagnosing this species: a first upper premolar that is tricuspidate, relatively large, and slightly triangular in occlusal view; absence of a sagittal crest; and a flat dorsal profile due to the absence of any angulation between the rostrum and braincase (Sanborn, 1937; Goodwin and Greenhall, 1961; Plumpton and Jones, 1992; Jones and Hood, 1993; Hood and Gardner, 2008). Measurements of *Rhynchonycteris* were provided by Husson (1962, 1978), Brosset and Charles-Dominique (1990), and Simmons and Voss (1998). No subspecies are currently recognized (Hood and Gardner, 2008).

Osgood (1914) and Fleck et al. (2002) correctly identified their specimens from Amelia ("Nazareth") and Nuevo San Juan, respectively, as *Rhynchonycteris naso*. Specimens from the Yavarí-Ucayali interfluve are morphologically indistinguishable from the French Guianan material reported by Simmons and Voss (1998) and from specimens from Bolivia (e.g., AMNH 248745), Brazil (e.g., AMNH 93941), Colombia (e.g., AMNH 78707), Ecuador (e.g., AMNH 67611), Trinidad and Tobago (e.g., AMNH 176618), and Venezuela (e.g., AMNH 78352).

Remarks: Ascorra et al. (1993) reported finding a group of about 20 individuals of *Rhynchonycteris naso* roosting under a bridge over a stream at Jenaro Herrera, and one individual was taken in a ground-level mistnet near a stream at this locality in 2012. At El Chino Village, three individuals were mistnetted above the town plaza in February 2019.

At Nuevo San Juan we captured four specimens in ground-level mistnets on river beaches or sandbars, but the remaining specimens from this locality were taken at roosts. All the roosts of *Rhynchonycteris naso* that we found near Nuevo San Juan were in exposed locations on the trunks or branches of dead trees partially submerged in the Río Gálvez: (1) a group of six individuals (of which one adult male was collected) were perching about 1.5 m above the water on 12 October 1999; (2) a group of three individuals (of which one adult male and one adult female were collected) were perching about 1 m above the water, also on 12 October 1999; and (3) a group of six or seven individuals (of which one adult female was collected) were perching at an unrecorded height above the water on 21 October 1999. In all three cases, the observed roosting groups of *R. naso* were unaccompanied by other bat species.

The roosts in which we found *Rhynchonycteris naso* near Nuevo San Juan closely resemble those previously reported in the literature for this very widespread species, which is almost always found over water (Husson, 1962; Tuttle, 1970; Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976; Brosset and Charles-Dominique, 1990).

Genus *Saccopteryx* Illiger, 1811

The genus *Saccopteryx* includes five species that collectively range from Mexico to Paraguay and southeastern Brazil (Simmons, 2005; Garbino, 2011; Owen et al., 2014; Simmons and Cirranello, 2020). References useful for identifying species of *Saccopteryx* include Sanborn (1937), Jones and Hood (1993), and Hood and Gardner (2008), all of which provide keys based on external and craniodental morphology. López-Baucells et al. (2018) additionally provided a key based on external characters only. All three species expected to occur in the Yavarí-Ucayali interfluve are represented in our material, and all three have also been detected by acoustic methods.

Saccopteryx bilineata (Temminck, 1838)

Figure 7A

Voucher material (total = 28): Isla Muyuy (MUSM 20978), Quebrada Blanco (MUSM 20980), Estación Biológica Madre Selva (MUSM

FIG. 7. Photographs of **A,** an adult female (ROM 122081) *Saccopteryx bilineata* and **B,** an adult male (ROM 122160) *S. leptura*, both captured at Jenaro Herrera. Photographs by Burton Lim.

TABLE 8

External and Craniodental Measurements (mm) and Weights (g) of *Saccopteryx bilineata* and *S. canescens* from the Yavarí-Ucayali Interfluve

	S. bilineata		*S. canescens*[c]
	Males[a]	Females[b]	
W	9.6 (7.8–10.5) 13	10.7 (8.1–13.3) 12	—
ToL	75.3 (67–80) 13	80.6 (75–86) 12	—
LT	18.4 (17–19) 13	20.3 (16–24) 12	—
HF	11.4 (10–13) 13	11.7 (10–13) 12	5.8 (4.8–7.3) 4
E	16.8 (14–19) 13	16.6 (15–19) 12	—
F	47.5 (46.0–50.0) 13	49.6 (47.0–55.0) 12	36.0 (34.5–37.1) 4
CCL	15.4 (15.3–15.5) 3	15.6 (15.0–16.0) 4	—
ZB	10.9, 11.1	10.9 (10.5–11.2) 4	—
MTL	7.2 (7.2–7.3) 3	7.4 (7.1–7.6) 4	—
BAM	7.6 (7.4–7.7) 3	7.6 (7.1–7.9) 4	—

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272673, 273082, 273102, 273127, 273152, 273166; CEBIOMAS 87; MUSM 5499, 13255, 13256, 15269–15271.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272672, 272811, 272863, 278510; MUSM 13252–13254, 15267, 15268, 20978, 30885, 30886.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for one male (MUSM 4206) and three female (MUSM 4354, 4357, 4358) specimens of *S. canescens*.

30885, 30886), Jenaro Herrera (AMNH 278510; CEBIOMAS 87; MUSM 5499), Nuevo San Juan (AMNH 272672, 272673, 272811, 272863, 273082, 273102, 273127, 273152, 273166; MUSM 13252–13256, 15267–15271), Quebrada Pantaleón (MUSA 15250), Río Blanco (MUSM 15076); see table 8 for measurements.

Unvouchered observations: During the Sierra del Divisor Rapid Biological Inventory, 15 individuals of *Saccopteryx bilineata* were captured at Divisor (Jorge and Velazco, 2006). Additionally, three individuals were captured at Quebrada Buenavista during the Yavarí Rapid Biological Inventory (Escobedo, 2003), and another was captured at Frog Valley. *Saccopteryx bilineata* was also recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Saccopteryx bilineata* is easily distinguished from other species in the genus by the following combination of traits: dorsal pelage and wing membranes blackish brown, paired longitudinal dorsal stripes white and conspicuous, forearm >44 mm, maxillary toothrow usually >7 mm, greatest width across molars (M3–M3) >7 mm (Emmons and Feer, 1997; Hood and Gardner, 2008; López-Baucells et al., 2018). Descriptions and measurements of *S. bilineata* were provided by Sanborn (1937), Goodwin and Greenhall (1961), Husson (1962, 1978), Brosset and Charles-Dominique (1990), Jones and Hood (1993), Simmons and Voss (1998), Yancey et al. (1998a), and Lim et al. (2005).

There is some disagreement concerning the recognition of subspecies in *Saccopteryx bilineata*. Koopman (1994) recognized two subspecies: *S. b. bilineata* (west-central Mexico to Colombia, Ecuador, eastern Peru, northern Bolivia, northern and eastern Brazil, southern Venezuela, and the Guianas) and *S. b. perspicillifer* (northern Venezuela and the island of Trinidad). By contrast, Yancey et al. (1998a), Simmons and Voss (1998), and Simmons (2005) did not recognize any subspecies for *S. bilineata*. Simmons and Voss (1998) noted that although significant geographic variation may exist among some populations of *S. bilineata*,

TABLE 9

Roosting Groups of *Saccopteryx bilineata* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
22 May1998	under fallen tree	unknown	unknown	1 ad. male, 4 ad. females
8 Jul 1998	exposed on standing tree	3	no	1 ad. male, 1 ad. female
11 Sep 1999	cavity in standing tree	1	yes	1 ad. male
20 Sep 1999	exposed on standing tree	4	no	1 ad. male, 1 ad. female
20 Sep 1999	cavity in standing tree	2	no	1 ad. female
28 Sep 1999	cavity in standing tree	1	yes	1 ad. male
30 Sep 1999	cavity in standing tree	3	no	1 ad. male
7 Oct 1999	exposed on standing tree	2	no	1 ad. male
15 Oct 1999	cavity in standing tree	1	yes	1 ad. male
21 Oct 1999	cavity in standing tree	1	yes	11 ad. males
25 Oct 1999	cavity in standing tree	1	yes	1 ad. male

none of the subspecies recognized by other authors (e.g., Hood and Gardner, 2008) appear to be justified by specimens they examined. For a more complete description of the trinomial history of *S. bilineata*, see Simmons and Voss (1998); we follow those authors in not recognizing subspecies in *S. bilineata*.

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their material from Jenaro Herrera, Nuevo San Juan, Quebrada Pantaleón, and the Río Blanco as *Saccopteryx bilineata*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the known range of intraspecific size variation.

Remarks: Twenty recorded captures of *Saccopteryx bilineata* at Jenaro Herrera were made in ground-level mistnets, five in elevated nets, and two at a roost (between buttresses of a standing tree). Of the 25 mistnet captures at this locality, 15 were made in primary forest, 5 in secondary vegetation, 4 in clearings, and 1 on a river beach. At Nuevo San Juan, all of our captures were made at roosts (table 9), where this species was invariably found in deeply shaded but not completely dark situations—for example, just inside rotted-out central cavities in standing trees. Most roosts were in well-drained primary forest (often on hillsides or hilltops), but two were found in seasonally inundated floodplain forest. Recorded heights of roosting groups were between 3 and 15 m above the ground (the single roosting group encountered on a fallen tree was sheltered among the buttresses of a huge trunk several meters above the ground). *Saccopteryx bilineata* was usually found roosting without other species nearby, but one roosting group shared a fallen tree with a roosting group of *Peropteryx pallidoptera*. At Divisor, a colony of about 15 individuals was found roosting in a cave (Jorge and Velazco, 2006).

Our observations from Nuevo San Juan are consistent with other descriptions of the roosts of this very widespread species, which are typically found either in the rotted-out central cavities of standing trees or in recesses between the buttresses of standing trees (Goodwin and Greenhall, 1961; Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976; Voss et al., 2016). In both situations, *Saccopteryx bilineata* occupies half-enclosed vertical concavities that are more heavily shaded than those occupied by its sympatric congener, *S. leptura*.

TABLE 10

External and Craniodental Measurements (mm) and Weights (g) of *Saccopteryx leptura* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	4.8 (4.2–5.4) 7	6.0 (4.0–12.0) 15
ToL	60.4 (56–65) 7	62.5 (56–65) 15
LT	14.7 (12–18) 7	15.0 (12–18) 15
HF	7.7 (7–8) 7	7.9 (6–9) 15
E	14.3 (13–16) 7	13.9 (13–16) 15
F	38.6 (38.0–40.0) 7	39.8 (38.0–42.0) 15
CCL	12.4 (12.0–12.8) 2	12.2 (11.9–12.4) 4
ZB	8.6	8.6 (8.3–9.1) 4
MTL	5.4 (5.2–5.6) 2	5.3 (5.1–5.5) 5
BAM	5.8	6.0 (5.7–6.2) 5

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273171; CEBIOMAS 88; MUSM 6975, 13257, 15272, 15273, 30910.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272722, 272723, 272865, 273101, 273105, 273136, 273167; MUSM 864, 5534, 6964, 13258, 13259, 15274–15276.

Saccopteryx canescens Thomas, 1901

VOUCHER MATERIAL (TOTAL = 4): Isla Padre (MUSM 4206, 4354, 4357, 4358); see table 8 for measurements.

UNVOUCHERED OBSERVATIONS: During the CEBIO bat course at Jenaro Herrera, *Saccopteryx canescens* was recorded using acoustic methods.

IDENTIFICATION: *Saccopteryx canescens* can easily be distinguished from other congeneric species by the following combination of features: dorsal pelage grayish or brownish, clearly bicolored, and lightly frosted with gray; paired whitish dorsal stripes indistinct, but visible; forearm <41 mm; length of maxillary toothrow ≤5 mm; greatest width across molars (M3–M3) <6 mm (Hood and Gardner, 2008; López-Baucells et al., 2018). Descriptions and measurements of *S. canescens* were provided by Sanborn (1937), Husson (1962, 1978), Brosset and Charles-Dominique (1990), Jones and Hood (1993), and Hood and Gardner (2008). No subspecies are currently recognized (Simmons, 2005; Hood and Gardner, 2008).

Our material from the Yavarí-Ucayali interfluve consists of fluid specimens that could be identified unambiguously as *Saccopteryx canescens* based on external characters.

REMARKS: No natural history information is available from our region.

Saccopteryx leptura (Schreber, 1774)

Figure 7B

VOUCHER MATERIAL (TOTAL = 23): Estación Biológica Madre Selva (MUSM 30910), Jenaro Herrera (CEBIOMAS 88; MUSM 864, 5534, 6964, 6975), Nuevo San Juan (AMNH 272722, 272723, 272865, 273101, 273105, 273136, 273167, 273171; MUSM 13257–13259, 15272–15276), Quebrada Lobo (MUSA 15125); see table 10 for measurements.

UNVOUCHERED OBSERVATIONS: An unspecified number of individuals of *Saccopteryx leptura* were observed at Quebrada Pobreza during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015). *Saccopteryx leptura* was also recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera.

IDENTIFICATION: *Saccopteryx leptura* can be distinguished from other congeneric species by

TABLE 11

Roosting Groups of *Saccopteryx leptura* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
21 Jun 1998	exposed on standing tree	4	no	1 ad. female
9 Jul 1998	unmodified foliage	4	no	2 ad. females
20 Sep 1999	exposed on standing tree	3	no	1 ad. male, 1 ad. female
20 Sep 1999	exposed on standing tree	2	yes	1 ad. male, 1 ad. female
7 Oct 1999	exposed on standing tree	2	yes	2 ad. females
21 Oct 1999	exposed on standing tree	3	no	1 male, 1 ad. female
22 Oct 1999	exposed on standing tree	1	yes	1 ad. male
1 Nov 1999	cavity in standing tree	2	no	1 ad. female

the following combination of characteristics: dorsal pelage uniformly brown, paired dorsal stripes usually distinct and beige or yellowish in color, forearm >36 mm; maxillary toothrow >5 mm; greatest width across molars (M3–M3) usually >6 mm (Emmons and Feer, 1997; Hood and Gardner, 2008; López-Baucells et al., 2018). Descriptions and measurements of *S. leptura* were provided by Sanborn (1937), Goodwin and Greenhall (1961), Husson (1962, 1978), Brosset and Charles-Dominique (1990), Jones and Hood (1993), Simmons and Voss (1998), Yancey et al. (1998b), Nogueira et al. (2002), Lim et al. (2005), and Garbino (2011). No subspecies are currently recognized (Simmons, 2005; Hood and Gardner, 2008).

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their material from Jenaro Herrera, Nuevo San Juan, and Quebrada Lobo, respectively, as *Saccopteryx leptura*. The voucher material from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, and measurements fall within the range of size variation previously documented for the species.

Remarks: Several captures of *Saccopteryx leptura* from our region are unaccompanied by ecological information, but one specimen from Jenaro Herrera was taken in a ground-level mist-net in a clearing, and another is said to have been collected 1.5 m above the ground as it roosted on a palm (*Bactris* sp.) frond in primary forest. All our specimens from Nuevo San Juan were collected at roosts (table 11), usually in shaded but exposed situations on standing trees; exceptionally, one roosting group was found beneath an unmodified leaf of the giant herb *Phenakospermum guyannense* (Strelitziaceae). Three roosts at this locality were in well-drained (hilltop or hillside) primary forest, three others were in seasonally flooded forest, and two were in old secondary vegetation; recorded heights of roosting groups were 2–8 m above the ground. *Saccopteryx leptura* was not found roosting with any other bat species near Nuevo San Juan.

Most of the roosts of *Saccopteryx leptura* that we found near Nuevo San Juan correspond closely to those previously reported elsewhere (e.g., by Bradbury and Emmons, 1974; Simmons and Voss, 1998). In general, these can be characterized as shallow, vertically oriented concavities that are better illuminated than those typically occupied by its sympatric congener *S. bilineata*; unlike *Rhynchonycteris naso*, which also roosts in exposed situations on standing trees, *Saccopteryx leptura* is not known to roost over water.

Family Noctilionidae Gray, 1821

The Neotropical family Noctilionidae (commonly known as bulldog bats) includes the sin-

TABLE 12

External and Craniodental Measurements (mm) and Weights (g) of *Noctilio albiventris* from the Yavarí-Ucayali Interfluve

	Males[a]	FMNH 89013 ♀	MUSM 15241 ♀	MUSM 15243 ♀
W	40.9 (39.0–42.3) 4	—	39.9	39.9
ToL	102.8 (95–111) 6	94	104	99
LT	20.2 (18–23) 6	14	20	21
HF	18.2 (17–19) 6	19	18	17
E	25.3 (24–27) 6	24	25	26
F	70.0 (68.0–71.0) 6	68.0	68.0	70.0
GLS	22.4 (22.1–23.1) 5	21.1	20.8	21.0
CIL	21.0 (20.5–21.6) 5	19.6	19.8	20.5
ZB	17.2 (16.8–17.8) 4	15.8	16.1	16.0
MTL	8.5 (8.3–8.8) 5	7.9	8.1	8.3
BAM	10.7 (10.5–10.8) 5	10.0	10.2	10.5

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273085, 273092; FMNH 89014, 89015; MUSM 5918, 15242.

gle genus *Noctilio* (Simmons, 2005; Gardner, 2008a; Simmons and Cirranello, 2020). Bulldog bats are characterized by a large number of distinctive traits including pointed and well-separated ears; a tragus with a bifurcated tip; nares that open anteriorly from a well-developed rhinarium that projects anteriorly beyond the lower lip; a chin with well-developed cross ridges of skin; buccal cheek pouches; an upper lip divided by two vertical grooves, one on each side of a prominent median ridge that extends from the rhinarium to the mouth; a tail that is approximately as long as the femur, with a terminal portion that projects above the much longer uropatagium; absence of incisive foramina; and a pair of large foramina in the posterior nasal region below the forehead (Simmons and Voss, 1998; Simmons and Conway, 2001; Gardner, 2008a; López-Baucells et al., 2018).

Two species of *Noctilio* are currently recognized, each containing several subspecies (Hood and Pitocchelli, 1983; Hood and Jones, 1984; Simmons, 2005; Gardner, 2008a). Molecular studies have confirmed monophyly of *N. leporinus*, but the same studies have conclusively demonstrated that *N. albiventris* (as traditionally recognized) is paraphyletic (Lewis-Oritt et al., 2001; Pavan et al., 2013; Khan et al., 2014). Patterns of variation in mtDNA gene sequences (cyt *b* and COI) indicate deep divergences among at least four lineages of *N. albiventris* (Lewis-Oritt et al., 2001; Pavan et al., 2013; Khan et al., 2014), but relationships among these groups remain ambiguous, and conflicting data from AFLP nuclear loci, zinc-finger Y, and zinc-finger X sequences have been interpreted as indicative of ongoing hybridization among lineages (Khan et al., 2014). Additional confusion has stemmed from an apparent genome-capture event involving the acquisition of an early-diverging *N. leporinus* mtDNA genome by a lineage of *N. albiventris* (see Khan et al., 2014). Due to the complexity of interpreting conflicting results from different genes, samples, and analytic methods; evidence of ongoing gene flow among populations; lack of evidence of ecological differences among lineages; and lack of comprehensive morphological analyses, no taxonomic changes have been made to date. In the most recent review of the genus, Khan et al. (2014) chose to recognize the lineages traditionally referred to *N. albiventris* as subspecies, despite the fact that the species

TABLE 13

Subspecific and Clade Composition of *Noctilio albiventris*

Davis, 1976	Gardner, 2008a	Pavan et al., 2013	Khan et al., 2014
affinis	*albiventris*[a]	Amazon (AMZ)	Albiventris 1
albiventris		Widespread (WSP)	Albiventris 2
cabrerai	*cabrerai*	Pantanal (PAN)	Albiventris 4
minor	*minor*	not evaluated	Albiventris 3

[a] Includes *affinis* as a junior synonym.

thus composed is not monophyletic. Although we generally agree with Khan et al. (2014), our review of specimens of the *N. albiventris* complex suggests that a revised subspecific classification is required, but to reassess and delimit the ranges of the subspecies will requiere a comprehensive revision including a denser geographic sampling and data from additional mitochondrial and nuclear markers.

Noctilio albiventris Desmarest, 1818

Voucher material (total = 9): Jenaro Herrera (MUSM 5918), Nuevo San Juan (AMNH 273085, 273092; MUSM 15241–15243), Quebrada Esperanza (FMNH 89013, 89014), San Vicente (FMNH 89015); see table 12 for measurements.

Unvouchered observations: None.

Identification: *Noctilio albiventris* is easily distinguished from *N. leporinus* by its smaller size (wingspan about 400 mm, length of foot <20 mm, forearm <70 mm, length of maxillary toothrow <8.5 mm) and feet that are shorter than the uropatagium (Hood and Pitocchelli, 1983; Gardner, 2008a; López-Baucells et al., 2018). Descriptions and measurements of *N. albiventris* were provided by Husson (1962, 1978), Davis (1976), Hood and Pitocchelli (1983), and Simmons and Voss (1998). Although our material can be confidently identified as *N. albiventris* by these criteria, the correct trinomen that applies to our material remains to be considered.

In his revision of *Noctilio albiventris*, Davis (1976) recognized four subspecies based on differences in size and coloration: *affinis* d'Orbigny, 1837; *albiventris* Desmarest, 1818; *cabrerai* Davis, 1976; and *minor* Osgood, 1910. Hood and Pitocchelli (1983) followed Davis' (1976) arrangement, but Gardner (2008a) reduced the number of recognized subspecies in *N. albiventris* to three, without discussion, by lumping *affinis* with *albiventris* (table 13). However, both Pavan et al. (2013) and Kahn et al. (2014) interpreted their respective molecular-phylogenetic results as supporting Davis's (1976) subspecies classification, thus recognizing *N. albiventris albiventris* and *N. a. affinis* as valid taxa. Unfortunately, they applied these names differently, and since the solution will require a comprehensive approach, we recommend against formally recognizing subspecies of *N. albiventris*.

Remarks: Ascorra et al. (1993: 540) reported a single capture of *Noctilio albiventris* "near a small artificial lake" at Jenaro Herrera; we assume that this specimen was caught in a mistnet, but whether at ground level or above was not explained. The only other ecological information about this species in our region is from Nuevo San Juan, where we found two roosting groups. The first, encountered on 11 September 1999, consisted of three individuals (of which only one adult male was collected) that were roosting in the company of *Molossus rufus* about 10 m above the ground inside a dead hollow tree on the bank of the Río Gálvez. The second group, encountered on 15 September 1999, consisted of 11 individuals, of which one adult male, four adult females, and five nursing young were captured; the 11th individual, which escaped, was presum-

TABLE 14

External and Craniodental Measurements (mm) of *Noctilio leporinus* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
ToL	125.8 (120–130) 4	116.7 (114–122) 7
LT	23.5 (21–26) 4	23.4 (22–26) 7
HF	29.5 (29–30) 6	27.4 (26–29) 9
E	27.8 (27–28) 4	27.1 (25–28) 7
F	84.2 (80.0–87.1) 6	83.8 (76.0–87.0) 9
GLS	26.9 (26.3–28.0) 4	25.0 (24.2–25.7) 7
CIL	24.3 (24.2–24.5) 3	23.3 (22.8–23.9) 7
ZB	19.5 (18.9–20.1) 4	18.2 (17.9–18.4) 6
MTL	10.4 (10.3–10.4) 4	9.8 (9.5–10.0) 7
BAM	12.8 (12.6–13.0) 4	12.0 (11.7–12.1) 7

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 89002, 89003, 89006, 89007, 89162, 89163.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 89004, 89005, 89008–89012, 89161, 89164.

ably the mother of the fifth offspring. These bats were roosting inside an abandoned woodpecker hole in an ant tree (*Triplaris* sp., Polygonaceae), also on the bank of the Gálvez; no other bat species was present in the latter roost.

Noctilio leporinus (Linnaeus, 1758)

Voucher material (total = 15): Quebrada Esperanza (FMNH 89002–89012, 89161–89164); see table 14 for measurements.

Unvouchered observations: None.

Identification: *Noctilio leporinus* is easily distinguished from *N. albiventris* by its larger size (wingspan about 500 mm; length of foot >25 mm; forearm >73 mm; length of maxillary toothrow >10 mm), including especially long hindlimbs, large feet, and well-developed claws that it uses for gaffing fish (Hood and Jones, 1984; Gardner, 2008a; López-Baucells et al., 2018). Descriptions and measurements of *N. leporinus* were provided by Husson (1962, 1978), Ceballos-Bendezú (1968), Davis (1973), Hood and Jones (1984), and Simmons and Voss (1998). Although three subspecies have traditionally been recognized (e.g., by Davis, 1973; Simmons, 2005; Gardner, 2008a), recent molecular studies support the recognition of only two: *N. l. leporinus* (in South America east of the Andes extending north into eastern Panama) and *N. l. mastivus* (distributed from Mexico south into the lowlands west of the Andes, with an additional population in Jamaica) (Pavan et al., 2013; Khan et al., 2014).

Ceballos-Bendezú (1968) correctly identified the specimens from Quebrada Esperanza as *Noctilio leporinus*. Our comparisons indicate that these specimens are morphologically indistinguishable from specimens from Bolivia (e.g., AMNH 210666), Brazil (e.g., AMNH 91943), and French Guiana (e.g., AMNH 265974). This result is congruent with the genetic findings of Pavan et al. (2013) and Khan et al. (2014) and suggests that the Quebrada Esperanza specimens should be referred to *N. l. leporinus*.

Remarks: No ecological information accompanies the unique series from Quebrada Esperanza, which was obtained by C. Kalinowski in 1957, but from the fact that these specimens were collected on three different dates (1 on 23 September, 10 on 25 September, and 4 on 26 September), we infer the probable occurrence of

multiple capture events. Because mistnets were seldom employed in the 1950s, these bats were probably shot at night by jacklight or taken from diurnal roosts.

Family Phyllostomidae Gray, 1825

Phyllostomidae, an ecologically diverse clade endemic to the Americas, includes omnivorous species as well as species variously specialized for insectivory, carnivory, nectarivory and pollenivory, frugivory, and sanguivory (Simmons and Voss, 1998; Wetterer et al., 2000). Phyllostomids are characterized by having a fleshy noseleaf, a well-developed tragus, a humerus with a well-developed trochiter and a double articulation with the scapula, digit II of the wing with a well-developed metacarpal and a small phalanx, digit III with three complete ossified phalanges, a fibula that is cartilaginous proximally, a friction lock on the digits of the feet, and oviductal folds limited to the extramural oviduct (Simmons and Voss, 1998; Gardner, 2008b; Cirranello et al., 2016). Gardner (2008c) and López-Baucells et al. (2018) provided keys to the genera and species of South American and Amazonian phyllostomids, respectively, based on external and craniodental characters. Sixty-six species in 32 genera are known from the Yavarí-Ucayali interfluve. Published records from localities adjacent to the Yavarí-Ucayali interfluve include another five phyllostomid species that might also occur in our study area (appendix 2).

Subfamily Carolliinae Miller, 1924

Eight species are currently recognized in the single genus (*Carollia*) comprising this subfamily (Simmons and Cirranello, 2020). Species in this subfamily are characterized by their medium size (forearm 34–45 mm), lack of facial or dorsal stripes, a moderately long muzzle, lack of a distinct boundary between the labial border of the horseshoe and the upper lip, a tail that extends about half the length of the uropatagium, a calcar that is shorter than the foot, broad upper molars with protocones on M1 and M2, and lower molars with well-developed protoconids and hypoconids (McLellan and Koopman, 2008; Cirranello et al. 2016). We recorded all three species of *Carollia* that are expected to occur in the Yavarí-Ucayali interfluve: *C. benkeithi, C. brevicauda,* and *C. perspicillata.*

Carollia benkeithi Solari and Baker, 2006

Voucher material (total = 22): Jenaro Herrera (CEBIOMAS 92; MUSM 820, 822, 825, 827, 852, 853, 5552), Nuevo San Juan (AMNH 272661, 272735, 272750, 272751, 272758, 272759, 272774, 272805, 272853; MUSM 13185), Quebrada Blanco (MUSM 21126), Quebrada Lobo (MUSA 15135), Quebrada Pantaleón (MUSA 15246, 15247); see table 15 for measurements.

Unvouchered observations: During the Yavarí Rapid Biological Inventory, individuals of *Carollia benkeithi* (previously identified as *C. castanea*) were captured at Quebrada Curacinha (two individuals) and Quebrada Limera (one individual) (Escobedo, 2003). One individual of *C. benkeithi* (also identified as *C. castanea*) was captured at Divisor during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006). One additional individual was captured at El Chino on 18 February 2019.

Identification: Although *Carollia benkeithi* can be distinguished from most other congeneric species by its small size (forearm <38 mm), it is easily confused with its allopatric congener *C. castanea*, which is similar in size and other external characteristics. However, *Carollia benkeithi* can be distinguished from *C. castanea* based on craniodental features, including a well-developed anterior cingulum on the second upper premolar (this cingulum is less developed in *C. castanea*), and a second upper premolar that is usually oriented in line with the long axis of the skull, resulting in an obvious "step" between the labial margins of the second premolar and the first molar (this "step" is less obvious in *C. castanea*; McLellan and Koopman, 2008). Descriptions and measurements of *C. benkeithi* were provided

TABLE 15

External and Craniodental Measurements (mm) and Weights (g) of *Carollia benkeithi* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	9.4 (7.7–10.0) 6	11.2 (8.5–19.0) 6
ToL	62.4 (57–66) 8	61.3 (55–68) 7
LT	10.9 (10–11) 8	9.6 (6–13) 7
HF	10.6 (8–12) 12	10.7 (8–12) 7
E	16.9 (15–18) 7	17.1 (17–18) 7
F	35.0 (34.0–36.0) 12	34.7 (34.0–35.0) 7
GLS	18.6 (18.3–19.1) 4	18.3 (18.0–18.7) 4
CIL	17.1 (16.6–17.5) 4	16.8 (16.3–17.1) 4
PB	5.3 (5.1–5.4) 4	5.2 (5.1–5.4) 4
BB	8.6 (8.4–8.8) 4	8.8 (8.6–8.9) 4
MB	9.7 (9.5–9.8) 4	9.5 (9.3–9.7) 4
MTL	6.2 (6.1–6.4) 4	6.0 (5.7–6.1) 4
BAM	7.1 (6.9–7.3) 4	6.8 (6.7–6.9) 4
BAC	4.3 (4.2–4.5) 4	4.1 (4.1–4.2) 4

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272661, 272735, 272750, 272758, 272805; MUSM 820, 822, 825, 827, 852, 5552, 13185.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272751, 272759, 272774, 272853; CEBIOMAS 94; MUSM 853, 21126.

by Solari and Baker (2006), McLellan and Koopman (2008), and Velazco and Patterson (2019). No subspecies are currently recognized (McLellan and Koopman, 2008).

Before the description of *Carollia benkeithi* in 2006, specimens of the smallest *Carollia* species from Nuevo San Juan and Jenaro Herrera were identified as *C. castanea* by Ascorra et al. (1993) and Fleck et al. (2002), respectively. However, Medina et al. (2015) correctly identified the specimens from Quebrada Lobo and Quebrada Pantaleón as *C. benkeithi*. Voucher specimens that we examined from the Yavarí-Ucayali interfluve conform to published descriptions of *C. benkeithi* in all respects, and measurements of this material fall within the range of size variation previously documented for the species.

Remarks: All of the 55 individuals of *Carollia benkeithi* accompanied by capture information from our region were mistnetted. Of these, 54 were taken in ground-level nets at Nuevo San Juan, including 20 in the understory of primary upland forest, 27 in secondary vegetation, 3 in clearings, 3 in a swampy mineral lick (*collpa*), 1 in a palm swamp (*aguajal*), and 1 on a beach. The individual captured at El Chino Village was taken at an unrecorded height in a "macro" net near the Río Tahuayo. It seems noteworthy that this common understory species was not captured during 16 nights of intensive mistnetting at Jenaro Herrera in January 2012, although Ascorra et al. (1993) had previously reported it (as *C. castanea*) from this locality.

Carollia brevicauda (Schinz, 1821)

Figure 8A

Voucher material (total = 30): Estación Biológica Madre Selva (MUSM 30977), Jenaro Herrera (AMNH 278470; MUSM 821, 823, 824, 826, 828, 849–851, 5543, 5919), Nuevo San Juan

FIG. 8. Photographs of **A,** an adult male (ROM 122257) *Carollia brevicauda* and **B,** an adult male (ROM 122230) *C. perspicillata*, both captured at Jenaro Herrera. Photographs by Burton Lim.

TABLE 16

External and Craniodental Measurements (mm) and Weights (g) of *Carollia brevicauda* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	14.1 (10.0–17.0) 11	14.8 (12.0–23.0) 11
ToL	65.3 (58–71) 10	64.8 (59–74) 11
LT	8.8 (6–11) 10	8.4 (6–11) 11
HF	12.1 (10–14) 13	11.3 (9–14) 14
E	19.2 (16–20) 10	18.5 (17–20) 11
F	37.8 (36.0–39.0) 13	37.5 (36.0–39.0) 14
GLS	20.7 (20.1–21.1) 6	20.6 (20.1–21.0) 7
CIL	19.2 (18.9–19.9) 6	19.1 (18.7–19.9) 7
PB	5.2 (5.1–5.5) 6	5.4 (5.2–5.6) 7
BB	9.3 (9.1–9.4) 6	9.3 (8.8–9.5) 7
MB	10.6 (10.2–10.8) 6	10.4 (10.1–10.8) 7
MTL	6.6 (6.4–7.0) 6	7.5 (6.5–6.9) 7
BAM	7.6 (7.3–8.2) 6	7.6 (7.3–8.0) 7
BAC	4.9 (4.6–5.1) 6	4.7 (4.6–4.9) 7

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272757, 272849, 272857, 273094, 273193, 278470; MUSM 821, 823, 824, 850, 5543, 5919, 13169, 15162.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272740, 272792, 273045, 273046; FMNH 89146; MUSM 826, 828, 849, 851, 13174, 15160, 15165, 21095, 30977.

(AMNH 272740, 272757, 272792, 272849, 272857, 273045, 273046, 273094, 273193; MUSM 13169, 13174, 15160, 15162, 15165), Quebrada Betilia (MUSA 15158, 15176), Quebrada Blanco (MUSM 21095), Quebrada Esperanza (FMNH 89146); see table 16 for measurements.

Unvouchered observations: During the Sierra del Divisor Rapid Biological Inventory, two individuals of *Carollia brevicauda* were captured at Divisor and another two individuals at Tapiche (Jorge and Velazco, 2006). One individual was captured at El Chino Village on 16 February 2019 and six were captured at Frog Valley on 17 February 2019. We captured 62 individuals from a single roosting group at Frog Valley on 20 February 2019. *Carollia brevicauda* was also recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Carollia brevicauda* can be distinguished from other congeneric species by the following combination of traits: forearm length 36–41 mm; pelage long, thick, and fluffy; forearm, tibia, and toes hairy; hair on nape of neck bicolored, with a broad, dark, basal band contrasting sharply with a broad, dirty-white band succeeding it distally; outer lower incisors not obscured by cingula of canines when lower jaw is viewed from directly above (dorsal view); labial outline of upper toothrow evenly curved, without a distinct notch; cuspids of m1 as well-developed as those of m2; crown of first lower incisor triangular in outline; trigonid of m1 distinctly narrower than talonid (Pine, 1972; McLellan and Koopman, 2008). Other descriptions and comparative measurements of *C. brevicauda* can be found in Brosset and Charles-Dominique (1990), Lim et al. (2005), McLellan and Koopman (2008), Velazco and Patterson (2019), and Lemos et al. (2020). No subspecies are currently recognized (McLellan and Koopman, 2008; Velazco, 2013).

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their

TABLE 17

Roosting Groups of *Carollia brevicauda* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
8 Jul 1998	cavity in fallen tree	2	yes	2 ad. males
4 Sep 1999	animal burrow/hole	unknown	unknown	3 ad. females
16 Sep 1999	under fallen tree	1	yes	1 ad. male
16 Sep 1999	cavity in standing tree	2	yes	1 ad. male
22 Oct 1999	cavity in fallen tree	unknown	unknown	1 ad. male
26 Oct 1999	animal burrow/hole	unknown	unknown	2 ad. females
5–8 Nov 1999	cavity in fallen tree	unknown	unknown	1 ad. male, 1 ad. female
5 Nov 1999	animal burrow/hole	unknown	unknown	1 ad. male
11 Nov 1999	cavity in fallen tree	unknown	unknown	1 ad. male

specimens from Jenaro Herrera, Nuevo San Juan, and Quebrada Betilia, respectively, as *Carollia brevicauda*. All voucher specimens from the Yavarí-Ucayali interfluve conform to previous descriptions of *C. brevicauda*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Of 74 recorded mistnet captures of *Carollia brevicauda* in our region, all were made at ground level (none was made in elevated nets). These ground-level mistnet captures included 28 in primary forest, 20 in secondary vegetation, 21 in clearings, 3 in a swampy mineral lick (*collpa*), 1 in a palm swamp (*aguajal*), and 2 on a river beach. The roosting group at Frog Valley occupied the large hollow log described earlier (see the account for *Peropteryx macrotis*); 62 individuals of *C. brevicauda* were captured as they emerged from this roost, which was shared with four other species (*P. macrotis*, *P. pallidoptera*, *Hsunycteris pattoni*, and *Trachops cirrhosus*), but many emerging bats evaded capture. We found nine additional roosting groups of *C. brevicauda* near Nuevo San Juan (table 17); most roosting groups occupied ground-level refugia in well-drained upland forest, but one group was roosting 3 m above the ground in the central cavity of a standing tree; one roost was found in seasonally flooded forest. *Carollia brevicauda* was seldom found roosting by itself at Nuevo San Juan: five roosts were shared with *Micronycteris microtis*, one with *Glossophaga soricina*, one with *Carollia perspicillata*, and one with both *Micronycteris matses* and *Peropteryx pallidoptera*.

Carollia perspicillata (Linnaeus, 1758)

Figure 8B

Voucher material (total = 76): Estación Biológica Madre Selva (MUSM 31265, 31266), Isla Padre (MUSM 4207–4209, 4214), Jenaro Herrera (AMNH 278466, 278501; CEBIOMAS 95, 96; MUSM 829–839, 854–857, 1054, 5544, 5548, 5920), Nuevo San Juan (AMNH 272663, 272665, 272692, 272737–272739, 272771, 272783, 272785, 272806, 272847, 272848, 273083, 273104, 273110, 273111, 273129, 273138, 273139; MUSM 11099, 13192, 15161, 15163, 15164, 15166–15170), Orosa (AMNH 73994–74005), Quebrada Betilia (MUSA 15159), Quebrada Blanco (MUSM 21094), Quebrada Esperanza (FMNH 89047, 89048), Quebrada Lobo (MUSA 15118, 15139); see table 18 for measurements.

Unvouchered observations: During the Sierra del Divisor Rapid Biological Inventory, one individual of *Carollia perspicillata* was captured at Divisor (Jorge and Velazco, 2006). An unspecified number of individuals of *C. perspicillata* were also captured at Anguila during the

TABLE 18

External and Craniodental Measurements (mm) and Weights (g) of *Carollia perspicillata* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	17.5 (12.0–25.0) 19	16.8 (14.0–22.0) 21
ToL	68.1 (58–74) 21	71.0 (60–78) 24
LT	8.4 (6–12) 21	10.8 (6–18) 24
HF	12.5 (10–14) 31	13.1 (9–15) 30
E	20.4 (17–22) 21	20.3 (18–22) 24
F	41.5 (39.0–44.0) 31	42.0 (40.0–44.6) 30
GLS	22.1 (21.3–22.9) 18	22.1 (21.4–22.8) 13
CIL	20.4 (19.9–21.0) 15	20.6 (19.9–21.1) 13
PB	5.4 (4.9–5.7) 20	5.4 (5.5–5.9) 15
BB	9.5 (9.1–10.0) 18	9.4 (9.0–10.2) 13
MB	10.9 (10.5–11.4) 18	10.8 (10.0–11.2) 13
MTL	7.6 (7.1–7.9) 18	7.6 (6.6–7.9) 14
BAM	7.7 (7.2–8.0) 16	7.8 (7.3–8.5) 11
BAC	5.0 (4.7–5.2) 20	4.9 (4.5–5.3) 15

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 73994–74001, 272692, 272739, 272771, 272785, 273085, 273110, 273111, 273129, 273139, 278466, 278501; CEBIOMAS 95; FMNH 89047; MUSM 829, 830, 832, 834, 836, 838, 839, 855, 857, 1054, 4207, 4208, 5544, 11099, 15166, 15168, 15170, 21094.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74002–74005, 272663, 272665, 272737, 272738, 272783, 272806, 272847, 272848, 273104, 273138; CEBIOMAS 96; FMNH 89048; MUSM 831, 833, 835, 837, 854, 856, 4209, 4214, 5548, 5920, 13192, 15161, 15163, 15164, 15167, 15169, 31265, 31266.

Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015). During the Yavarí Rapid Biological Inventory, this species was captured at Quebrada Buenavista (four individuals), Quebrada Curacinha (two individuals) and Quebrada Limera (three individuals) (Escobedo, 2003). We captured two individuals at El Chino Village on 16 February 2019, and another two individuals at Tahuayo Farm on 19 February 2019. *Carollia perspicillata* was also recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Carollia perspicillata* can be distinguished from other congeneric species by the following combination of traits: forearm ≥39 mm; pelage relatively short; forearm and toes naked or only sparsely haired; half or more of the outer lower incisors obscured by cingula of canines when the lower jaw is viewed from directly above; V-shaped lower jaw, with rami straight in occlusal view; and maxillary toothrow length >7.4 mm (Pine, 1972; Cloutier and Thomas, 1992; McLellan and Koopman, 2008). Other descriptions and comparative measurements of *C. perspicillata* can be found in Goodwin and Greenhall (1961), Husson (1962, 1978), Brosset and Charles-Dominique (1990), Cloutier and Thomas (1992), Lim et al. (2005), McLellan and Koopman (2008), Velazco and Patterson (2019), and Lemos et al. (2020).

McLellan (1984) and Cloutier and Thomas (1992) did not recognize any subspecies of *Carollia perspicillata*, but McLellan and Koopman (2008) recognized three: *C. p. azteca* (Central America, Trinidad and Tobago, north and west of the Amazon Basin in Venezuela, Colombia, and Ecuador), *C. p. perspicillata* (across the Amazon Basin in the Guianas, Venezuela, Brazil, and eastern Colombia,

TABLE 19

Roosting Groups of *Carollia perspicillata* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
2 Sep 1999	cavity in standing tree	2	no	1 ad. male
11 Sep 1999	cavity in standing tree	1	yes	1 ad. male
16 Sep 1999	cavity in standing tree	1 or 2	no	1 ad. female
20 Sep 1999	cavity in standing tree	12?	no	1 ad male, 5 ad. females
22 Sep 1999	cavity in standing tree	1	yes	1 ad. male
22 Sep 1999	cavity in standing tree	7?	no	3 ad. males
28 Sep 1999	cavity in standing tree	2	yes	1 ad. male, 1 ad. female
1 Oct 1999	cavity in standing tree	1	yes	1 ad. male
7 Oct 1999	cavity in standing tree	"many"	no	1 ad. male
11 Oct 1999	inside hollow log	8	no	1 ad. male, 2 ad. females
22 Oct 1999	cavity in standing tree	4	no	1 ad. female, 1 juv. (sex unrecorded)
29 Oct 1999	cavity in standing tree	unknown	unknown	1 ad. male

Ecuador, Peru, and Bolivia), and *C. p. tricolor* (Paraguay, southern Bolivia and Brazil, and northern Argentina). However, Velazco (2013) analyzed samples from throughout the range of this species ($N = 90$) and found low intraspecific cytochrome *b* divergence and little or no phylogeographic structure, suggesting that the recognition of subspecies is not justified. Therefore, we do not recognize any subspecies of *C. perspicillata*.

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their material from Jenaro Herrera, Nuevo San Juan, Quebrada Betilia, and Quebrada Lobo as *Carollia perspicillata*. All the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *C. perspicillata*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Of 140 recorded mistnet captures of *Carollia perspicillata* in our region, 124 were taken in ground-level nets and 16 were taken in elevated nets. Of these mistnet captures, 39 were in primary forest, 61 were in secondary vegetation, 28 were in clearings, 8 were in a palm swamp (*aguajal*), and 4 were on river beaches.

We found 12 roosts of *Carollia perspicillata* near Nuevo San Juan (table 19), usually in the rotted-out central cavities of standing trees, but one roost was inside a hollow log. Six roosts at this locality were in seasonally flooded forest, three were in primary upland forest, one was in a palm swamp, another was in liana forest, and one was in a small (0.5 ha) blowdown. Recorded heights of roosts in standing trees ranged from 1.5 to 25 m above the ground. *Carollia perspicillata* was often found roosting alone, but three roosts (all in standing trees) were shared with other species. Of these, one was shared with *Lampronycteris brachyotis* and one with both *Phyllostomus hastatus* and *Molossus rufus*; the third roost, which contained only *Carollia perspicillata* on 22 September 1999, was shared with *Lampronycteris brachyotis* when it was revisited on 14 October 1999, and the same roost was shared with both *Lampronycteris brachyotis* and *Trachops cirrhosus* when it was revisited a second time on 25 October 1999.

Although *Carollia perspicillata* often inhabits caves and manmade refugia (buildings, culverts, bridges, etc.) in other parts of its extensive geographic range (Goodwin and Greenhall, 1961;

FIG. 9. Photograph of an adult female (ROM 122098) *Desmodus rotundus* captured at Jenaro Herrera. Photograph by Burton Lim.

Handley, 1976; Fleming, 1988), our observations from Nuevo San Juan suggest that, in minimally disturbed and caveless Amazonian landscapes, this species usually roosts in hollow trees.

Subfamily Desmodontinae Wagner, 1840

Commonly known as vampires, three extant desmodontine species, each in its own genus, are currently recognized (Kwon and Gardner, 2008; Simmons and Cirranello, 2020). Members of this subfamily are characterized by having a reduced noseleaf with a smooth internarial region and thin, free, flaplike lateral edges; two chin pads with smoothly rounded edges, one on either side of the midline; a uropatagium that is reduced to a narrow, ridgelike band of skin; lack of an external tail; sharp, caninelike incisors; reduced molars and premolars; and wing digit III with three bony phalanges (Kwon and Gardner, 2008; Cirranello et al. 2016). We recorded two vampire species in the Yavarí-Ucayali interfluve; the third species, *Diaemus youngii*, is expected to occur in our region (appendix 2), but it has yet to be collected or observed there.

Desmodus rotundus (Geoffroy St.-Hilaire, 1810)

Figure 9

Voucher material (total = 8): Estación Biológica Madre Selva (MUSM 31781), Isla Muyuy (MUSM 21145), Jenaro Herrera (AMNH 278473; CEBIOMAS 98; MUSM 845, 846, 867, 868); see table 20 for measurements.

Unvouchered observations: We captured a single individual of *Desmodus rotundus* at El Chino Village on 16 February 2019. This species was also recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Desmodus rotundus* can be easily distinguished from other vampires by the

TABLE 20

External and Craniodental Measurements (mm) and Weights (g) of *Desmodus rotundus* from the Yavarí-Ucayali Interfluve

	AMNH 278473 ♂	MUSM 21145 ♂	Females[a]
W	30.0	28.0	37.0 (29.0–46.0) 4
ToL	76	80	81.0 (75–84) 4
HF	15	15	17.2 (15–20) 6
E	18	20	19.0 (18–20) 4
F	58.0	60.0	62.7 (60.0–66.0) 6
GLS	22.0	23.5	23.9 (23.4–24.4) 2
CIL	21.3	21.8	22.0 (21.6–22.4) 2
PB	5.1	5.6	5.4 (5.3–5.4) 2
BB	11.5	12.0	12.2 (11.8–12.5) 2
ZB	11.2	12.3	11.7 (11.5–11.9) 2
MTL	3.5	3.6	3.4 (3.2–3.5) 2
BAM	6.1	6.5	6.3 (5.9–6.7) 2

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of CEBIOMAS 98; MUSM 845, 846, 868, 867, 31781.

following characteristics: thumb greatly elongated (>13 mm), longer than hind foot, and with two basal pads; dark wingtips; calcar reduced to a wartlike excrescence; ventral sulcus present on tongue; inner lower incisors bilobed; and a single upper molar on each side (Goodwin and Greenhall, 1961; Kwon and Gardner, 2008; Cirranello et al., 2016; López-Baucells et al., 2018). Descriptions and measurements were provided by Goodwin and Greenhall (1961), Husson (1962, 1978), Swanepoel and Genoways (1979), Greenhall et al. (1983), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), and Velazco and Patterson (2019). Some authors (e.g., Greenhall et al., 1983; Kwon and Gardner, 2008) have recognized two subspecies: *D. r. murinus* (northwestern Mexico south to the Pacific lowlands and western slope of the Andes in Colombia, Ecuador, and Peru) and *D. r. rotundus* (Venezuela, Trinidad, the Guianas, the Amazon basin of Colombia, Ecuador, Peru, Brazil, and Bolivia, south to Paraguay, Uruguay, Chile, and Argentina). In contrast, other authors (e.g., Koopman, 1988; Simmons, 2005) have noted that, although considerable morphological variation exists across the distributional range of *D. rotundus*, this variation is not sufficiently clearly patterned to warrant assigning subspecies status to any populations. Although analyses of mitochondrial DNA sequences support the recognition of five distinct geographical clades (Martins et al., 2007; Martins et al., 2009), morphometric studies and limited analyses of nuclear DNA have thus far not provided sufficient corroborating evidence that these clades are anything more than haplogroups (Martins et al., 2009; Martins and Hubbe, 2012). Accordingly, we follow Koopman (1988) and Simmons (2005) in not recognizing subspecies of *D. rotundus*.

Ascorra et al. (1993) correctly identified the material he reported from Jenaro Herrera. All the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Desmodus rotundus*, with measurements that fall within the range of size variation previously documented for this species.

Remarks: Of 20 recorded captures of *Desmodus rotundus* in the Yavarí-Ucayali interfluve, 17 were made in ground-level mistnets, 2 in elevated mistnets, and 1 in a harp trap. Of these

captures, 9 were made in primary forest, 8 in secondary vegetation, and 3 in clearings. No roosting groups of this species were encountered during our study. Wilson et al. (1996) plausibly attributed the abundance of this species at Jenaro Herrera to the local abundance of cattle among farms adjacent to the research station.

Diphylla ecaudata Spix, 1823

Voucher material (total = 3): Quebrada Betilia (MUSA 15164), Quebrada Lobo (MUSA 15132), Quebrada Pantaleón (MUSA 15248).

Unvouchered observations: None.

Identification: *Diphylla ecaudata* can be distinguished from other vampire species by the following characteristics: thumb small (usually <13 mm) and lacking basal pads, calcar stout (not a wartlike excrescence), uropatagium well furred, ventral fur unicolored, tail absent, occlusal margin of lower inner incisors with four lobes, occlusal margin of lower outer incisors with three lobes, two upper incisors and two lower molars present on each side (Kwon and Gardner, 2008; Cirranello et al., 2016; López-Baucells et al., 2018). Descriptions and measurements of *D. ecaudata* were provided by Swanepoel and Genoways (1979), Greenhall et al. (1984), Kwon and Gardner (2008), and Velazco and Patterson (2019). Two subspecies are currently recognized: *D. e. centralis* (southern US southward through eastern Mexico and Central America) and *D. e. ecaudata* (Venezuela, Colombia, Ecuador, Peru, Bolivia, and Brazil, with the exception of the central Amazon basin) (Greenhall et al., 1984; Kwon and Gardner, 2008).

Medina et al. (2015: fig. 2D) correctly identified their specimens as belonging to the nominotypical subspecies.

Remarks: All examined specimens of *Diphylla ecaudata* are from the Zona Reservada Sierra del Divisor, where they were presumably taken in mistnets (Medina et al., 2015), but no other capture information is currently available to us. No roosting groups of this typically cave-roosting species (Kwon and Gardner, 2008) were encountered during our fieldwork.

Subfamily Glossophaginae Bonaparte, 1845

A total of 14 genera and 37 species are currently recognized in the subfamily Glossophaginae (Simmons, 2005; Griffiths and Gardner, 2008a; Nogueira et al., 2012; Simmons and Cirranello, 2020). Members of this subfamily are characterized by a long and slender muzzle; a long and highly extensible tongue, the tip of which is covered with hairlike papillae, and the lateral margins of which lack grooves; a lower lip that is divided by a deep vertical groove; a short or absent tail; zygomatic arches that are weak or incomplete; premolars with reduced cusps and styles; anteroposteriorly elongated molars; and upper molars lacking hypocones (Griffiths and Gardner, 2008a; Cirranello et al., 2016). We recorded four species in the Yavarí-Ucayali interfluve (*Anoura caudifer*, *Choeroniscus minor*, *Glossophaga bakeri*, *G. soricina*), but another two species (*Anoura geoffroyi*, *Lichonycteris degener*) are also expected to occur in our region (appendix 2).

Anoura caudifer (É. Geoffroy St.-Hilaire, 1818)

Figure 10A

Voucher material (total = 4): Jenaro Herrera (MUSM 5585), Nuevo San Juan (MUSM 15277), Quebrada Betilia (MUSA 15157), Quebrada Pantaleón (MUSA 15257); see table 21 for measurements.

Unvouchered observations: None.

Identification: *Anoura caudifer* is a widespread species distributed across French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, Bolivia, northern Argentina, and northern and southern Brazil (Griffiths and Gardner, 2008a; Oprea et al., 2009). This species is easily distinguished from other congeners by external and craniodental features including the following traits: presence of a short tail; a well-developed calcar that is slightly shorter than the foot; a wide, sparsely haired uropatagium with a large U-shaped cutout from the trailing edge; a lower lip that protrudes less than 3 mm beyond

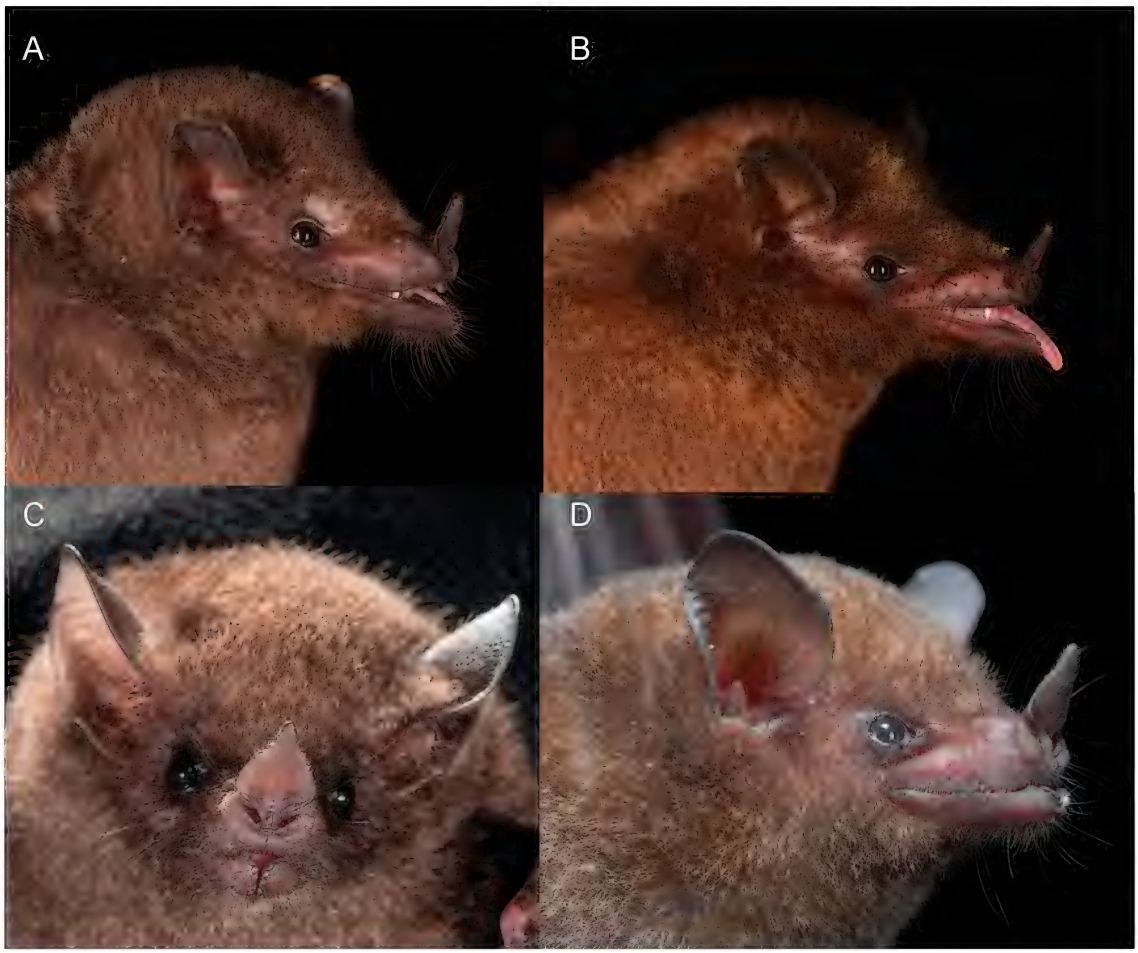


FIG. 10. Photographs of **A,** an adult *Anoura caudifer* captured at Quebrada Blanco; **B,** an adult *Choeroniscus minor* captured at Quebrada Blanco; **C,** an adult *Glossophaga bakeri* captured at El Chino Village; and **D,** an adult female (ROM 122150) *G. soricina* captured at Jenaro Herrera. Photographs by Marco Tschapka (A, B), Brock Fenton (C), and Burton Lim (D).

the upper lip; a mesopterygoid fossa with a median keel that is not flattened posteriorly and that usually extends into a septum between the basisphenoid pits; and a last upper premolar that lacks a medial internal cusp (Griffiths and Gardner, 2008a; Oprea et al., 2009; López-Baucells et al., 2018). Descriptions and measurements of *A. caudifer* were provided by Husson (1962), Handley (1984), Brosset and Charles-Dominique (1990), Molinari (1994), Simmons and Voss (1998), Lim et al. (2005), Mantilla-Meluk and Baker (2006), Oprea et al. (2009), and Velazco and Patterson (2019). No subspecies are currently recognized (Simmons, 2005; Griffiths and Gardner, 2008a; Oprea et al., 2009).

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their material of *Anoura caudifer* from Jenaro Herrera, Nuevo San Juan, Quebrada Betilia, and Quebrada Pantaleón. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *A. caudifer*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: The only specimen of *Anoura caudifer* accompanied by capture information

TABLE 21

External and Craniodental Measurements (mm) and Weights (g) of *Anoura caudifer* and *Choeroniscus minor* from the Yavarí-Ucayali Interfluve

	A. caudifer	*C. minor*	
	Females[a]	Males[b]	Females[c]
W	9.0, 11.6	8.6, 7.4	10.5 (7.9–15.0) 6
ToL	63, 68	66, 64	65.0 (60–70) 6
LT	5, 6	11, 10	8.3 (6–13) 6
HF	10, 11	9, 8	9.0 (7–10) 6
E	14, 16	12, 11	11.7 (10–13) 6
F	36.7, 37.0	35.0, –	34.7 (34–35) 6
GLS	21.9, 22.0	22.8, –	23.1 (22.5–24.2) 3
CIL	21.6, 21.3	22.2, –	22.8 (22.1–23.6) 3
BB	9.0, 8.3	8.4, –	8.4 (8.3–8.6) 3
MB	9.4, 8.7	8.4, –	8.5 (8.3–8.6) 2
ZB	9.9, 8.8	—	—
MTL	7.2, 7.9	7.6, –	8.0 (7.6–8.3) 3
BAM	5.8, 5.8	4.2, –	4.4 (4.2–4.7) 3
BAC	–, 4.0	3.7, –	3.8 (3.7–3.9) 3

[a] MUSM 5585, 15277.
[b] MUSM 15172, 15173.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273066, 273106; MUSM 862, 5586, 13195, 15171.

from our region is an adult female that was found roosting beneath the undercut bank of a small stream in primary upland forest near Nuevo San Juan on 30 September 1999. The diurnal refugia of *Anoura caudifer* have seldom been described, but Griffiths and Gardner (2008a: 228) reported that this species was found roosting beneath the undercut banks of forest streams at another Amazonian locality.

Choeroniscus minor (Peters, 1868)

Figure 10B

Voucher material (total = 9): Jenaro Herrera (MUSM 862, 5586), Nuevo San Juan (AMNH 273066, 273106; MUSM 13195, 15171–15173), Quebrada Lobo (MUSA 15127); see table 21 for measurements.

Unvouchered observations: None.

Identification: Before the revision by Simmons and Voss (1998), specimens of *Choeroniscus minor* were referred to several species (*C. inca*, *C. minor*, and *C. intermedius*) that were diagnosed primarily by the length of the rostrum (Koopman, 1978). After reviewing specimens (including holotypes) throughout the distribution of these nominal taxa, Simmons and Voss (1998) concluded that they represent a single species for which *C. minor* (Peters, 1868) is the oldest available name. *Choeroniscus minor* is distinguished from other congeners by the following combination of characteristics: rostrum shorter than braincase, posterolateral margin of palate unnotched, pterygoids moderately inflated, forearm ≤38 mm, greatest length of skull >21 mm, and maxillary toothrow >7.5 mm (Simmons and Voss, 1998; Griffiths and Gardner, 2008a; Solmsen and Schliemann, 2008). This species exhibits marked sexual size dimorphism,

with females being larger than males (Husson, 1962; Brosset and Charles-Dominique, 1990; Simmons and Voss, 1998; Solmsen, 1998; Solmsen and Schliemann, 2008). Additional descriptions and measurements of *C. minor* have been provided by Goodwin and Greenhall (1961), Husson (1962), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Lim et al. (2005), and Solmsen and Schliemann (2008). No subspecies are currently recognized (Simmons and Voss, 1998; Griffiths and Gardner, 2008a; Solmsen and Schliemann, 2008).

The Jenaro Herrera specimens were originally identified as *Choeroniscus intermedius* by Ascorra et al. (1993), but Fleck et al. (2002) and Medina et al. (2015) correctly identified their specimens from Nuevo San Juan and Quebrada Lobo, respectively, as *C. minor*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *C. minor*, with measurements that fall within the range of size variation now documented for the species. However, it is noteworthy that one specimen (MUSM 15172) possesses an extra pair of lower molars.[5]

Remarks: The only specimens of *Choeroniscus minor* accompanied by ecological data from our region were collected at two roosts near Nuevo San Juan. The first, encountered on 8 September 1999, consisted of two adult females under the buttresses of a fallen tree in secondary growth at the edge of a Matses swidden. The second roost, encountered on 20 September 1999, consisted of two adult males and one adult female perched on the underside of an unmodified frond of the stemless palm *Attalea racemosa*, about 1 m above the ground, in primary hilltop forest.

Our discovery of *Choeroniscus minor* roosting in foliage represents atypical behavior; all previously described roosts of this species have been found under fallen trees or inside hollow logs (Sanborn, 1954; Patterson, 1992; Simmons and Voss, 1998; Rengifo et al., 2013).

[5] Supernumerary teeth usually occur unilaterally in glossophagines, but supernumerary teeth are known to occur bilaterally in numerous other bat taxa, especially nectarivorous and frugivorous species (Slaughter, 1970; Phillips, 1971; Bergmans and Van Bree, 1972; Bergmans, 1976; Giannini and Simmons, 2007).

Glossophaga bakeri Webster and Jones, 1987

Figure 10C

Voucher material (total = 7): Isla Muyuy (MUSM 21150–21156); see table 22 for measurements.

Unvouchered observations: We captured two individuals *Glossophaga bakeri* at Tahuayo Farm on 19 February 2019 and another four individuals at El Chino Village on 21 February 2019.

Identification: *Glossophaga bakeri* was originally described as a subspecies of *G. commissarisi* based on seven specimens from Amazonian localities in Brazil, Colombia, and Peru. Webster (1993) subsequently delimited two other subspecies: *G. c. commissarisi*, distributed from southeastern Mexico to southern Panama, and *G. c. hespera*, which occurs only in western Mexico. Our review of voucher material from the Yavarí-Ucayali interfluve together with specimens from other subspecies of *G. commissarisi* and other South American species of *Glossophaga* suggests that *bakeri* should be recognized as a distinct species.

Descriptions and measurements of *Glossophaga bakeri* (as *G. commissarisi bakeri*) were provided by Webster and Jones (1987) and Webster (1993). This is a medium-sized glossophagine with dark-brown dorsal fur. The dorsal hairs are bicolored, with a long, light-brown base (comprising about 90% of the length of each hair) and a short, dark-brown terminal band. The ventral fur is similar to the dorsal fur in coloration, with the exception of the terminal band, which is paler than the terminal band of the dorsal fur. The dorsum of the uropatagium is naked, the calcar is shorter than the hind foot, and the dorsal surface of the foot is sparsely covered with short hairs. The dermal pads on the chin are separated by a wide cleft and the rostrum is short and wide. The presphenoid ridge (or keel) is

TABLE 22

External and Craniodental Measurements (mm) and Weights (g) of *Glossophaga bakeri* and *G. soricina* from the Yavarí-Ucayali Interfluve

	G. bakeri		*G. soricina*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	8.3 (6.8–9.2) 5	8.8, 9.8	8.3 (6.0–10.3) 12	9.8 (7.0–13.0) 9
ToL	58.2 (56–61) 5	58, 61	58.4 (50–68) 14	62.0 (57–65) 13
LT	6.2 (5–7) 5	6, 5	6.2 (3–9) 14	6.4 (4–11) 13
HF	9.2 (8–10) 5	9, 10	9.0 (5–11) 14	9.7 (7–12) 13
E	15.2 (14–17) 5	15, 14	13.5 (12–15) 14	14.2 (13–15) 13
F	35.0 (34.3–36.0) 5	37.4, 35.8	34.4 (34.0–35.5) 14	35.5 (34.0–37.6) 13
GLS	19.8 (19.1–20.2) 5	20.5, 20.4	19.8 (19.1–20.2) 11	20.4 (19.6–21.3) 12
CIL	19.3 (19.0–19.7) 4	20.0, 19.1	18.8 (18.5–19.4) 8	19.3 (18.8–20.2) 12
BB	8.6 (8.3–9.0) 5	8.8, 8.6	8.3 (7.9–8.7) 11	8.5 (8.2–8.8) 12
MB	9.0 (8.8–9.2) 5	9.1, 8.9	8.6 (8.2–8.8) 11	8.8 (8.3–9.2) 12
ZB	9.5 (9.3–9.8) 5	9.6, –	8.9 (8.7–9.1) 4	9.1 (9.0–9.2) 5
MTL	6.9 (6.6–7.1) 5	7.2, 7.0	6.8 (6.5–7.1) 11	7.1 (6.7–7.5) 11
BAM	5.6 (5.4–5.8) 5	5.9, 5.7	5.2 (4.9–5.5) 11	5.4 (5.3–5.5) 10
BAC	4.0 (3.9–4.1) 5	4.0, 3.9	3.6 (3.3–3.9) 11	3.7 (3.3–4.0) 11

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 21150, 21152–21154, 21156.

[b] MUSM 21151, 21155.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74012, 273191, 273194; CEBIOMAS 99; FMNH 89110; MUSM 5521, 5522, 5540, 5587, 5930, 15196, 15198, 15199, 21157, 21159, 21160.

[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74104, 74105, 74111, 74112, 273097, 273128, 278497; FMNH 89111; MUSM 5511, 5538, 5539, 5588, 5939, 13204, 15195, 15197, 21158.

weakly developed. The upper and lower incisors are evenly spaced, and the upper canine and each of the upper premolars are separated from one another by gaps (diastemata). The second upper premolar has a well-developed posterior cusp, the upper and lower molars are robust, and the M1 parastyle is moderately developed.

Glossophaga bakeri is morphologically distinct from *G. commissarisi*. Externally, the dermal pads on the chin of *Glossophaga bakeri* are separated by a wide cleft, whereas the homologous cleft is narrower in *G. commissarisi*. Cranially, the presphenoid ridge (or keel) is weakly developed in *G. bakeri*, whereas it is flattened in *G. commissarisi*. Dentally, the upper incisors in *G. bakeri* are evenly spaced, whereas in *G. commissarisi* the inner upper incisors are in contact or almost in contact with each other. The lower incisors of *G. bakeri* are evenly spaced, whereas they are separated into two pairs by a conspicuous gap in *G. commissarisi*. The second upper premolar of *G. bakeri* has a well-developed posterior cusp, whereas accessory cusps are absent in *G. commissarisi*. The parastyle of M1 is reduced in *G. bakeri*, whereas it is well developed and directed posterolabially in *G. commissarisi*.

Thus restricted, *Glossophaga commissarisi* is known only from Middle America, whereas *G. bakeri* is endemic to western Amazonia; both species cooccur with the ubiquitous *G. soricina* (see below), which is the only other congener known to occur in eastern Amazonia. Although Griffiths and Gardner (2008a: 239) reported a specimen of *G. commissarisi* from Guyana, we examined the

specimen in question (USNM 565513) and reidentified it as *G. soricina*.[6] In the absence of any clear pattern of geographical variation, we do not recognize any subspecies of *G. bakeri*.

Remarks: The two specimens of *Glossophaga bakeri* from Tahuayo Farm were taken in ground-level mistnets in old secondary vegetation. We used hand nets to capture four males that were members of a single roosting group of about a dozen individuals in an abandoned concrete building at El Chino Village. No natural roosts of this species were encountered during our study.

Glossophaga soricina (Pallas, 1766)

Figure 10D

Voucher material (total = 34): Isla Muyuy (MUSM 21157, 21158), Jenaro Herrera (AMNH 278497; CEBIOMAS 99; MUSM 5511, 5521, 5522, 5538–5540, 5587, 5588, 5930, 5939), Nuevo San Juan (AMNH 273097, 273128, 273191, 273194; MUSM 13204, 15195–15199), Orosa (AMNH 74012, 74014, 74015, 74111, 74112), Quebrada Blanco (MUSM 21159, 21160), Quebrada Esperanza (FMNH 89110, 89111), Quebrada Lobo (MUSA 15133); see table 22 for measurements.

Unvouchered observations: An unspecified number of individuals of *Glossophaga soricina* were captured at Wiswincho during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015).

Identification: *Glossophaga soricina* occurs throughout most of the rainforested lowlands of cis-Andean South America (Hoffmann et al., 2019; Calahorra-Oliart et al., 2021). This species is distinguished from other congeners by its domed, rounded braincase; well-developed mandibular symphyseal ridge; large, procumbent inner upper incisors that extend anteriorly well beyond the outer upper incisors; a well-developed parastyle on M1; crowded lower incisors that are usually in contact with one another and with the canines; well-developed mesostyles on m1 and m2; and relatively dark pelage (Alvarez et al., 1991; Webster, 1993; Griffiths and Gardner, 2008a; Calahorra-Oliart et al., 2021). Descriptions and measurements were provided by Miller (1913a), Goodwin and Greenhall (1961), Husson (1962), Alvarez et al. (1991), Webster (1993), Simmons and Voss (1998), Lim et al. (2005), Griffiths and Gardner (2008a), Velazco and Patterson (2019), and Calahorra-Oliart et al. (2021). Following a recent revision that elevated formerly conspecific populations from west and north of the Andes to species level, no subspecies are currently recognized in *G. soricina* (Calahorra-Oliart et al., 2021).

Ceballos-Bendezú (1968), Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their specimens from Quebrada Esperanza, Jenaro Herrera, Nuevo San Juan, and Quebrada Lobo, respectively, as *Glossophaga soricina*. All the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the nominotypical subspecies, and measurements of our material fall within the range of size variation previously documented for that taxon.

Remarks: Specimens of *Glossophaga soricina* accompanied by capture data from our region include six individuals taken in ground-level mistnets and three taken in elevated nets; of these, eight were netted in clearings and one was netted in primary forest. We found three roosts of *Glossophaga soricina* near Nuevo San Juan. The first (occupied by three individuals, of which one adult female was captured on 17 September 1999) was beneath the undercut bank of a small stream in seasonally flooded forest; another roost (occupied by two individuals, of which one adult female was captured on 1 October 1999) was inside a hollow log in seasonally flooded forest; and the third roost (occupied by an unknown number of individuals, of which two adult males, two adult females, and three immature males were captured between 5 and 8 November 1999) was inside a

[6] Griffiths and Gardner's (2008a) account of South American *Glossophaga* does not mention the epithet *bakeri*, either as the name of a valid taxon or as a synonym, an obvious lapsus.

hollow log in primary upland forest. The first two roosts were occupied only by *G. soricina*, but the third was shared with *Carollia brevicauda*.

Glossophaga soricina has been found roosting in a wide range of situations in South America and seems appropriately considered a roost generalist (Voss et al., 2016).

Subfamily Glyphonycterinae Baker et al., 2016

Five species in three genera (*Glyphonycteris*, *Trinycteris*, *Neonycteris*) are currently recognized in this subfamily (Baker et al., 2003; Dávalos et al., 2014; Baker et al., 2016; Cirranello et al., 2016; Simmons and Cirranello, 2020). These taxa were traditionally classified as members of the genus *Micronycteris* in the subfamily Phyllostominae (Simmons, 1996, 2005), but molecular data have shown that *Glyphonycteris* and *Trinycteris* do not group with other species of *Micronycteris* and, indeed, are not even closely related to other "phyllostomines." Instead, these taxa form a clade that nests among primarily plant-feeding lineages elsewhere in the phyllostomid tree (Baker et al., 2003; Dávalos et al., 2012, 2014). Baker et al. (2003) named this clade Glyphonycterinae, but it was not diagnosed and its name not made available until the joint publications of Baker et al. (2016) and Cirranello et al. (2016). Members of this subfamily are small to large bats (forearm 36–58 mm) that have a simple noseleaf with the spear equal to or longer than twice the height of the horseshoe; additionally, the rib of the spear is restricted to its proximal part; there is no distinct boundary between the labial border of horseshoe and the upper lip; the chin has two dermal pads with smoothly rounded lateral margins; the calcar is shorter than the foot; the outer upper incisors are in contact with the canines; and the second lower premolar is short, less than ¼ the height of the first and third lower premolars (Cirranello et al., 2016). All three species expected to occur in the Yavarí-Ucayali interfluve are represented among the voucher specimens we examined.

Glyphonycteris daviesi (Hill, 1965)

Figure 11

Voucher material (total = 4): Nuevo San Juan (AMNH 273179, 273180; MUSM 15200, 15201); see table 23 for measurements.

Unvouchered observations: None.

Identification: *Glyphonycteris daviesi* can be distinguished from other species of *Glyphonycteris* by its unicolored-brownish dorsal fur, larger size (forearm >50 mm, greatest length of skull >25 mm), one pair of upper incisors that are nearly the same length as the upper canines, and lower-incisor crowns that are antero-posteriorly elongated and transversely narrow (Williams and Genoways, 2008; López-Baucells et al., 2018). Descriptions and measurements of *G. daviesi* were provided by Hill (1965), Tuttle (1970), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Brosset and Charles-Dominique (1990), Pine et al. (1996), Simmons (1996), Simmons and Voss (1998), Lim et al. (2005), and Morales-Martínez and Suárez-Castro (2014). No subspecies are currently recognized (Williams and Genoways, 2008).

Fleck et al. (2002) correctly identified the specimens from Nuevo San Juan as *Glyphonycteris daviesi*. Their voucher material conforms to previous descriptions of *G. daviesi*, with measurements that fall within the previously documented range of size variation for the species.

Remarks: The specimens of *Glyphonycteris daviesi* from Nuevo San Juan were members of a single roosting group consisting of five individuals, of which one adult male, two adult females, and one juvenile female were collected on 26 October 1999. This group occupied the rotted-out central cavity of a standing tree in hillside primary forest; no other species was found roosting with *G. daviesi*.

Only two roosts of *Glyphonycteris daviesi* have previously been described in the literature (Tuttle, 1970; Solari et al., 1999). In both cases, roosting individuals were found in hollow standing trees, which, on the basis of our additional observation from Nuevo San Juan, would appear to be the typical diurnal refuge of this infrequently collected species.

FIG. 11. Photograph of an adult *Glyphonycteris daviesi* captured at Quebrada Blanco. Photograph by Marco Tschapka.

Glyphonycteris sylvestris (Thomas, 1896)

Voucher material (total = 1): Nuevo San Juan (AMNH 15202); see table 23 for measurements.

Unvouchered observations: None.

Identification: *Glyphonycteris sylvestris* can be distinguished from other congeneric species by its tricolored dorsal fur, smaller size (forearm <44 mm, greatest length of skull <22 mm), two pairs of upper incisors that are nearly the same length as the canines, outer upper incisors that are almost hidden by the canine cingula in occlusal view, and lower incisors that are similar in anteroposterior and transverse dimensions (Williams and Genoways, 2008; López-Baucells et al., 2018). Descriptions and measurements of *G. sylvestris* were provided by Sanborn (1949a), Goodwin and Greenhall (1961), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Simmons (1996), Simmons and Voss (1998), Lim et al. (2005), and Morales-Martínez and Suárez-Castro (2014). No subspecies are currently recognized (Williams and Genoways, 2008).

Fleck et al. (2002) correctly identified the specimens from Nuevo San Juan as *Glyphonycteris sylvestris*. Their voucher material conforms to previous descriptions of *G. daviesi*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: The single specimen of *Glyphonycteris sylvestris* from our region was part of a roosting group that occupied the rotted-out central cavity of a large standing tree in primary upland forest; many bats were observed to be roosting about 20 m above the ground in the hollow interior, of which only this adult male was collected on 19 October 1999.

In addition to our observation from Nuevo San Juan, several other reports (Goodwin and Green-

TABLE 23

External and Craniodental Measurements (mm) and Weights (g) of *Glyphonycteris daviesi, G. sylvestris,* and *Trinycteris nicefori* from the Yavarí-Ucayali Interfluve

	G. daviesi		*G. sylvestris*	*T. nicefori*	
	AMNH 273180 ♂	Females[a]	MUSM 15202 ♂	Males[b]	MUSM 13213 ♀
W	24.2	24.1 (15.2–29.5) 3	10.2	8.5 (7.4–10.0) 7	8.9
ToL	76	74.0 (70–77) 3	64	63.3 (57–69) 8	71
LT	9	8.3 (8–9) 3	10	10.5 (9–13) 8	12
HF	17	17.0 (17–17) 3	11	11.4 (10–13) 8	14
E	30	29.0 (26–31) 3	20	17.8 (17–19) 8	18
F	56.0	55.0 (50.0–58.0) 3	39.0	38.0 (36.7–39.0) 8	41
GLS	—	—	—	19.8 (19.5–20.0) 5	—
CIL	—	—	—	18.8 (18.4–19.0) 5	—
BB	—	—	—	8.3 (8.0–8.6) 5	—
MB	—	—	—	8.8 (8.6–9.1) 5	—
ZB	—	—	—	9.8 (9.2–10.5) 5	—
MTL	—	—	—	7.5 (7.4–7.8) 5	—
BAM	—	—	—	6.7 (6.5–7.0) 5	—
BAC	—	—	—	3.6 (3.3–3.9) 5	—

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273179; MUSM 15200, 15201.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272802, 272840; MUSM 5551, 13214, 21302–21305.

hall, 1961; Handley, 1976; Williams and Genoways, 1980a) suggest that hollow standing trees are typical roosts of *Glyphonycteris sylvestris*.

Trinycteris nicefori Sanborn, 1949

Voucher material (total = 9): Jenaro Herrera (MUSM 5551), Nuevo San Juan (AMNH 272802, 272840; MUSM 13213, 13214), Quebrada Blanco (MUSM 21302–21305); see table 23 for measurements.

Unvouchered observations: None.

Identification: *Trinycteris nicefori* is easily distinguished from other phyllostomids by the following combinations of characteristics: the chin has a pair of dermal pads, one on each side of the midline; the dorsal fur is tricolored and either grayish brown or orange; a faint, pale middorsal stripe is present on the lower back; the ear is >16 mm and tapers to a blunt point; of the metacarpals, the fourth is the shortest and the third is the longest; the calcar is shorter than the foot; the upper incisors are procumbent, not in line with the canines, distinctly shorter and narrower than those teeth, and not chisel shaped; and the first upper premolar lacks accessory cusps (Sanborn, 1949a; Wetterer et al., 2000; Williams and Genoways, 2008; López-Baucells et al., 2018). Descriptions and measurements of *T. nicefori* were provided by Sanborn (1949a), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Brosset and Charles-Dominique (1990), Simmons (1996), Simmons and Voss (1998), Lim et al. (2005), and Rocha et al. (2013). No subspecies are currently recognized (Williams and Genoways, 2008).

Ascorra et al. (1993) and Fleck et al. (2002) correctly identified their material from Jenaro Herrera and Nuevo San Juan, respectively, as *Trinycteris nicefori*. The voucher material we exam-

ined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *T. nicefori*, with measurements that fall within the range of size variation previously documented for the species. Both of the color phases ("red" and "gray") described by Sanborn (1949a) are present among specimens collected in our region.

Remarks: The only four specimens of *Trinycteris nicefori* accompanied by ecological information from our region were captured in ground-level mistnets in the understory of primary upland forest near Nuevo San Juan.

Subfamily Lonchophyllinae Griffiths, 1982

Twenty species in five genera (*Hsunycteris*, *Lionycteris*, *Lonchophylla*, *Platalina*, *Xeronycteris*) are currently recognized in this subfamily (Parlos et al., 2014; Moratelli and Dias, 2015; Baker et al., 2016; Cirranello et al., 2016; Simmons and Cirranello, 2020). Lonchophyllines are small to medium-sized bats (with forearms measuring 30–60 mm) characterized by a long muzzle; a wide, teardrop-shaped noseleaf; a long, extensible tongue with a deep longitudinal groove along each lateral surface; an elongated skull with incomplete zygomatic arches; large upper incisors with the inner pair usually more than twice the size of the outer teeth; and lower incisors with spatulate, trifid tips (Griffiths and Gardner, 2008b; Cirranello et al., 2016). At least four lonchophyllines occur in the Yavarí-Ucayali interfluve; three of these are species of *Hsunycteris* vouchered by collected specimens, and the fourth is *Lionycteris spurrelli*, which is vouchered by a photograph. No other lonchophyllines have geographic ranges that overlap or adjoin our region.

Genus *Hsunycteris* Parlos et al., 2014

Four species are currently recognized in *Hsunycteris* (Velazco et al., 2017; Simmons and Cirranello, 2020). These taxa were traditionally classified within the genus *Lonchophylla* (e.g., by Griffiths and Gardner, 2008b), but molecular analyses have shown that the species now referred to *Hsunycteris* do not group with species of *Lonchophylla,* nor are these genera even sister taxa. Instead, *Hsunycteris* seems to be sister to a clade containing all the other lonchophylline genera (Parlos et al., 2014). Velazco et al. (2017) provided a key to the species of the genus. We recorded all three of the *Hsunycteris* species expected to occur in the Yavarí-Ucayali interfluve.

Hsunycteris dashe Velazco et al., 2017

Figure 12A

Voucher material (total = 3): Nuevo San Juan (AMNH 273165; MUSM 15206, 15211); see table 24 for measurements.

Unvouchered observations: None.

Identification: *Hsunycteris dashe* was recently described from the Yavarí-Ucayali interfluve and is not currently known to occur elsewhere. It can be distinguished from other members of the genus by its large size (forearm 35–36 mm); long (≥9 mm), bicolored dorsal fur; noseleaf with a central rib that is weakly defined but extends all the way from the upper lip to the apex; chin with dermal papillae arranged in a V and separated by a wide basal cleft; broad rostrum; infraorbital foramen with a lateral margin that does not project beyond the rostral outline in dorsal view; large outer upper incisors that are only slightly smaller than the inner upper incisors; third upper premolar with a weakly developed lingual cusp; and well-developed, labially oriented M1 parastyle (fig. 12A; Velazco et al., 2017).[7] No subspecies are currently recognized.

Remarks: All our specimens of *Hsunycteris dashe* were collected from two roosts near Nuevo San Juan, both of them beneath the undercut banks of small streams in upland primary forest. The first roost, encountered on 2 September 1999, contained a single adult female; the second, encountered on 21 October 1999, contained

[7] Note that Velazco et al. (2017: 3) incorrectly defined P5 as the "2nd upper premolar." In fact, P5 is the posteriormost of the three teeth in this series.

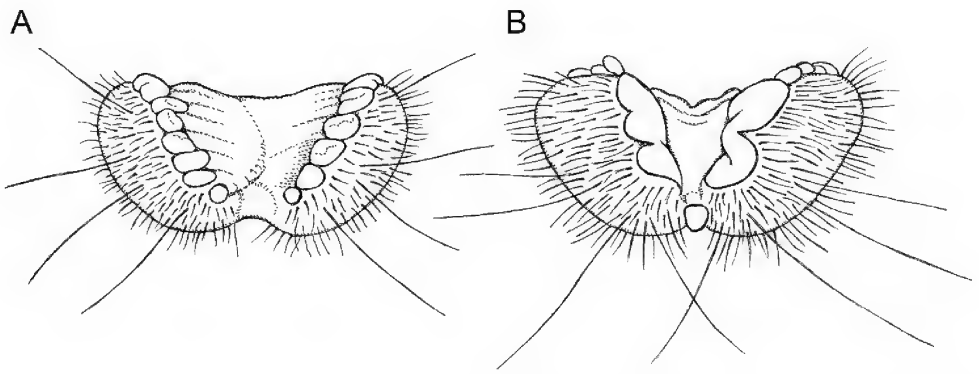


FIG. 12. Anterior views of the chins of *Hsunycteris dashe* (**A**, AMNH 273165) and *H. pattoni* (**B**, MUSM 13205) illustrating taxonomic differences in the arrangement of the dermal papillae. In *H. dashe* the chin exhibits several small dermal papillae arranged in a "V" and separated by a wide basal cleft. In *H. pattoni*, however, the dermal papillae on the chin are larger and are not separated by a basal cleft.

three individuals, of which one adult female and her nursing young were collected.

Hsunycteris pattoni
(Woodman and Timm, 2006)

Figure 12B, 13A

Voucher material (total = 27): Estación Biológica Madre Selva (MUSM 31927–31930), Jenaro Herrera (AMNH 278465, 278500; CEBIOMAS 100, 101; MUSM 863, 5523, 5541, 5542, 5589, 5932, 5933, 5940), Nuevo San Juan (AMNH 273069, 273093, 273124–273126; MUSM 13205, 15207–15210), Quebrada Blanco (MUSM 21173); see table 24 for measurements.

Unvouchered observations: We captured a single individual of *Hsunycteris pattoni* at El Chino village on 16 February 2019, eight individuals at Tahuayo Farm on 19 February 2019, and four individuals at Frog Valley on 20 February 2020.

Identification: *Hsunycteris pattoni* is easily distinguished from other members of the genus by its paler, reddish-brown dorsal fur; the dermal papillae on the chin are larger and not separated by a wide basal cleft (fig. 12B); metacarpal V is shorter than metacarpal IV; the rostrum and postorbital region are narrower and only slightly inflated; lack of lateral projections in the postorbital region; posterior margin of infraorbital foramen between the first and second upper premolars; septum between basisphenoid pits narrow; dentary long and slender, with a narrow angular process; second upper premolar lingual cusp absent; third upper premolar lingual cusp narrow; M1 parastyle well developed; reduced protocone basin on M1 and M2; extent of maxillary posterior to M3 less than the length of M3; lower incisors small and narrow; m1 paracristid notch weakly developed or absent; m2 hypoconid narrow (Woodman and Timm, 2006; Velazco et al., 2017). Descriptions and measurements of *H. pattoni* were provided by Woodman and Timm (2006), Mantilla-Meluk et al. (2009, 2010), and Velazco et al. (2017). No subspecies are currently recognized (Woodman and Timm, 2006).

Specimens of *Hsunycteris pattoni* from Jenaro Herrera were identified as *Lonchophylla mordax* by Ascorra et al. (1993), and the specimens from Nuevo San Juan were identified as *L. thomasi* by Fleck et al. (2002). All their material and additional specimens that we examined from the Yavarí-Ucayali interfluve (listed above) conform to the diagnosis of *H. pattoni* as summarized in the key by Velazco et al. (2017), with measurements that fall within the range of size variation previously documented for this species.

FIG. 13. Photographs of **A,** an adult male (ROM 122182) *Hsunycteris pattoni* captured at Jenaro Herrera; and **B,** an adult *H. thomasi* captured at Quebrada Blanco. Photographs by Burton Lim (A) and Marco Tschapka (B).

TABLE 24

External and Craniodental Measurements (mm) and Weights (g) of *Hsunycteris dashe*, *H. pattoni*, and *H. thomasi* from the Yavarí-Ucayali Interfluve

	H. dashe	*H. pattoni*		*H. thomasi*	
	Females[a]	Males[b]	Females[c]	Males[d]	Females[e]
W	10.2, 9.3	6.5 (3–8.5) 15	8.0 (5–15) 11	7.1 (6.4–9.0) 4	–, 6
ToL	65, 61	59.7 (52–58) 15	59.7 (57–65) 11	57.8 (53–60) 4	62, 60
LT	8, 12	7.2 (5–9) 15	7.7 (5–10) 11	7.0 (5–9) 4	5, 6
HF	10, 11	8.7 (8–10) 15	8.4 (7–11) 11	7.5 (7–8) 4	10, 7
E	14, 13	13.1 (12–16) 15	14.0 (12–16) 11	15.5 (14–18) 4	15, 15
F	36.0, 35.0	32.1 (31.0–34.0) 15	32.7 (31.0–34.0) 11	31.0 (30.4–32.0) 4	32.0, 33.0
GLS	20.5, 20.8	20.7 (20.4–21.1) 4	20.7 (19.9–21.8) 8	21.1 (20.8–21.9) 4	21.1, 20.9
CIL	19.8, 19.8	20.2 (20.0–20.3) 4	20.2 (19.3–20.7) 8	20.4 (19.8–21.1) 4	–, 20.5
BB	8.5, 8.7	8.3 (8.3–8.4) 4	8.2 (7.9–8.5) 8	8.3 (8.1–8.5) 4	8.5, 8.2
MB	8.8, 8.9	8.7 (8.5–8.9) 4	8.6 (8.2–9.4) 8	8.6 (8.4–8.9) 4	–, 8.6
MTL	6.5, 6.4	7.0 (6.7–7.2) 4	6.9 (6.7–7.1) 8	7.1 (6.9–7.2) 4	6.8, 7.1
BAM	5.5, 5.5	5.4 (5.3–5.5) 4	5.3 (5.0–5.7) 8	5.4 (5.1–5.5) 4	5.2, –
BAC	4.1, 4.0	3.7 (3.6–3.7) 4	3.6 (3.5–3.9) 8	3.8 (3.6–4.0) 4	3.6, 3.7

[a] AMNH 273165; MUSM 15206.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273069, 273124; CEBIOMAS 101; MUSM 5523, 5541, 5542, 5933, 5940, 15207, 15208, 15210, 31927–31930.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273093, 273126, 278465, 278500; CEBIOMAS 100; MUSM 863, 5589, 5932, 13205, 15209, 21173.
[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 5509, 5931, 21170, 21171.
[e] FMNH 87070; MUSM 21172.

Remarks: Of 13 recorded mistnet captures of *Hsunycteris pattoni* from our region, all were made in ground-level nets, and a single harp-trap capture (at Tahuayo Farm) was also made at ground level. Five of these nocturnal captures were made in primary forest, eight in secondary vegetation, and one in a clearing. At Frog Valley, we captured four females as they emerged from a hollow-log roost that they shared with *Peropteryx macrotis* (see above), *P. pallidoptera*, *Carollia brevicauda*, and *Trachops cirrhosus*; because many emerging bats escaped, we do not know whether the entire roosting group of *H. pattoni* was captured. We found six roosts of *H. pattoni* near Nuevo San Juan (table 25), all of them inside or under fallen trees. Four roosts were in primary upland forest (in well-drained valley bottoms or on hillsides), but one was in seasonally flooded forest and another was in a palm swamp. *Hsunycteris pattoni* was not found roosting with any other species at Nuevo San Juan.

Our roost observations are apparently the first to be associated with this species.

Hsunycteris thomasi (Allen, 1904)

Figure 13B, 14

Voucher material (total = 6): Jenaro Herrera (MUSM 5509, 5931), Quebrada Blanco

FIG. 14. *Hsunycteris* cf. *thomasi* feeding on a *Chelonanthus alatus* (Gentianaceae) at Jenaro Herrera. Photograph by Marco Tschapka.

(MUSM 21170–21172), Santa Cecilia (FMNH 87070); see table 24 for measurements.

Unvouchered observations: We captured four individuals of *Hsunycteris thomasi* at El Chino village on 17 February 2019.

Identification: *Hsunycteris thomasi* occurs from Panama throughout most of northern South America to eastern Bolivia and central Brazil (Griffiths and Gardner, 2008b; Reid, 2009). Although Parlos et al. (2014) reported analyses of mitochondrial and nuclear markers indicating that populations of *H. thomasi* are paraphyletic with respect to *H. pattoni*, no morphological traits appear to distinguish members of the two clades of *H. thomasi* recovered in their molecular analyses (Velazco et al., 2017). Sequence data from the holotype of *H. thomasi* should be obtained to determine which of the two *Hsunycteris* clades the epithet properly applies to, and which clade represents an undescribed taxon, but our attempts to do so have thus far been unsuccessful (Velazco et al., 2017). Currently, *H. thomasi* is best regarded as a potential species complex, although the extent of lineage differentiation remains uncertain.

Populations of *Hsunycteris thomasi* (as this species is currently understood; see above) can be distinguished from other congeners by the following combination of characteristics: small size (forearm ≤34.5 mm); metacarpal V subequal to metacarpal IV in length; dermal papillae on chin arranged in a V but not separated by a wide basal cleft; narrow rostrum; postorbital region lacking lateral projections; lateral margin of infraorbital foramen not projecting beyond rostral outline in dorsal view; extent of maxillary posterior to M3 greater than the length of M3; dentary deep; angular process broad; outer upper incisors small; second upper premolar lingual cusp present; third upper premolar lingual cusp

TABLE 25

Roosting Groups of *Hsunycteris pattoni* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
8 Sep 1999	under fallen tree	unknown	unknown	1 ad. male
9 Sep 1999	inside hollow log	2	yes	1 ad. male, 1 ad. female
16 Sep 1999	inside hollow log	3	no	1 ad. male, 1 ad. female
29 Sep 1999	inside hollow log	4	no	1 ad. male, 1 ad. female, 1 juv. female
30 Sep 1999	inside hollow log	1	yes	1 ad. female
15 Oct 1999	inside hollow log	5	no	2 ad. males

broad; M1 parastyle well developed; lower incisors small and narrow; m1 paracristid notch weakly developed or absent; m2 hypoconid narrow (Velazco et al., 2017). Descriptions and measurements of *H. thomasi* have been provided by Husson (1962, 1978), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Albuja V and Gardner (2005), Woodman and Timm (2006), and Velazco et al. (2017). No subspecies are currently recognized (Velazco et al., 2017).

Specimens from Jenaro Herrera were identified as *Lonchophylla mordax* (MUSM 5931) or as *L. thomasi* (MUSM 5509) by Ascorra et al. (1993). Velazco et al. (2017) reidentified Ascorra et al.'s material and other voucher specimens from the Yavarí-Ucayali interfluve, all of which conform to previous descriptions of *H. thomasi*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Of six recorded captures of *Hsunycteris thomasi* accompanied by ecological data from our region, four were in ground-level mist-nets and two were in elevated nets; five of these captures were in clearings and one was in primary forest. No roosting groups of this species were encountered during our study.

Lionycteris spurrelli Thomas, 1913

Voucher material: None.

Unvouchered observations: A single male individual of this species was captured and photographed at Wiswincho in October 2014 during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015).

Identification: *Lionycteris* is a monotypic genus that occurs from eastern Panama to Bolivia and Brazil (Griffiths and Gardner, 2008b). *Lionycteris spurrelli* can be easily distinguished from other lonchophyllines by the following traits: muzzle narrow and elongated, with short vibrissae; noseleaf with a short, wide spear; chin with dermal papillae arranged in a V and separated by a wide basal cleft ending ventrally in an unpaired papilla; pinnae small and rounded; base of dorsal pelage darker than tips; plagiopatagium attached near base of toe; greatest length of skull <21 mm; rostrum shorter than braincase; upper premolars short and broad; and both upper premolars with well-developed lingual cusps (Solmsen, 1998; Woodman and Timm, 2006; Griffiths and Gardner, 2008b; López-Baucells et al., 2018). Descriptions and measurements of *L. spurrelli* were provided by Phillips (1971), Carter and Dolan (1978), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Gregorin and Ditchfield (2005), Woodman and Timm (2006), Woodman (2007), and Velazco and Patterson (2019). No subspecies are currently recognized (Griffiths and Gardner, 2008b).

The photographs of the male individual captured at Wiswincho exhibit the external morphological characteristics of *L. spurrelli* (e.g., dark brown fur; short rostrum; short, wide noseleaf; chin with dermal papillae arranged in a V ending

ventrally in an unpaired papilla; small, rounded pinnae; and plagiopatagium attached near base of toe). Based on our examination of the photographs we see no reason to doubt Escobedo-Torres's (2015) identification of the individual he captured and released at Wiswincho.

Remarks: According to Escobedo-Torres (2015), bats were only captured using mistnets during the Tapiche-Blanco Rapid Biological Inventory, but whether *Lionycteris spurrelli* was taken at ground level or in the canopy is unknown. Unfortunately, electronically recorded field notes from this expedition have been corrupted, so no additional information is now available concerning this unique capture.

TABLE 26

External Measurements (mm) and Weights (g) of *Lampronycteris brachyotis* from the Yavarí-Ucayali Interfluve

	Males[a]	MUSM 15203 ♀
W	13.4 (7.9–16.1) 5	14.3
ToL	68.0 (60–72) 5	76
LT	11.6 (9–14) 5	11
HF	13.0 (12–14) 5	13
E	17.4 (16–18) 5	18
F	39.8 (37.0–42.0) 5	44.0

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273146, 273147, 273177; MUSM 15204, 15205.

Subfamily Micronycterinae Van den Bussche, 1992

Two genera (*Micronycteris* and *Lampronycteris*) and 12 species are currently recognized in the subfamily Micronycterinae (Williams and Genoways, 2008; Larsen et al., 2011; Siles et al., 2013; Baker et al., 2016; Cirranello et al., 2016; Simmons and Cirranello, 2020). Members of this subfamily are small to medium-sized bats (forearm 32–46 mm) that can be recognized by the following combination of traits: noseleaf simple, with spear equal to or longer than twice the height of horseshoe; labial border of horseshoe fused to upper lip, forming a thickened ridge; chin with two dermal pads with smoothly rounded lateral margins; calcar equal to or longer than foot; ventral fur unicolored; and outer upper incisor in contact with canine (Cirranello et al., 2016). We recorded all seven micronycterine species expected to occur in the Yavarí-Ucayali interfluve.

Lampronycteris brachyotis (Dobson, 1879)

Voucher material (total = 6): Nuevo San Juan (AMNH 273146, 273147, 273177; MUSM 15203–15205); see table 26 for measurements.

Unvouchered observations: A single specimen (MUSM 12989) of *Lampronycteris brachyotis* collected at Jenaro Herrera was reported by Solari et al. (1999), who published external and craniodental measurements consistent with their identification of this distinctive species. Unfortunately, the specimen has since been lost.

Identification: *Lampronycteris brachyotis*, the only member of its genus, is a widespread species with a patchy distribution that extends from southern Mexico to eastern Brazil (Medellín et al., 1985; Marciente and Calouro, 2009; Reid, 2009; Scultori et al., 2009a; Oliveira and Faria, 2015). This species is easily distinguished from other micronycterines by the following combination of traits: ears not connected by a transverse band of skin across the top of the head; pinnae pointed, each with a concavity on the posterior border near the tip; ear length ca.16 mm; dorsal fur bicolored; yellow-orange to reddish unicolored fur on the throat and upper chest; third metacarpal longer than fourth metacarpal, which is longer than the fifth; calcar shorter than foot; rostrum inflated, especially in the lacrimal region; shallow basisphenoid pits; upper inner incisors less than half the height of upper canines; upper incisors chisel shaped and in line with canines; and trifid lower incisors (Sanborn, 1949a; Goodwin and Greenhall, 1961; Simmons, 1996; Williams and Genoways, 2008; López-Baucells et al., 2018). Descriptions and measurements of *L. brachyotis* were provided by

Sanborn (1949a), Goodwin and Greenhall (1961), Swanepoel and Genoways (1979), Medellín et al. (1985), Simmons (1996), Marciente and Calouro (2009), Scultori et al. (2009a), Oliveira and Faria (2015), and Brandão et al. (2016). No subspecies are currently recognized (Williams and Genoways, 2008).

Fleck et al. (2002) correctly identified the specimens from Nuevo San Juan, all of which conform to previous descriptions of *Lampronycteris brachyotis* and have measurements that fall within the range of size variation previously documented for the species.

Remarks: All the specimens of *Lampronycteris brachyotis* from Nuevo San Juan were collected from two roosts, both of of which were in the rotted-out central cavities of large standing trees. The first, which was visited three times in 1999, was in seasonally flooded forest. An unknown number of bats occupied this roost, where they were difficult to see as they clustered about 18 m above the ground in the dark, chimneylike interior. On 22 September 1999 only *Carollia perspicillata* was collected in this roost, but on 14 October we collected several *Lampronycteris brachyotis* (two adult males, one adult female, and one juvenile male) in addition to *Carollia perspicillata*, and on 25 October we collected another *Lampronycteris brachyotis* (an adult male) in addition to *Carollia perspicillata* and *Trachops cirrhosus*. The second roost, encountered on 29 October 1999, was in a palm swamp; many bats occupied the hollow interior of this tree, including an unknown number of individuals of both *Lampronycteris brachyotis* (of which one adult male was collected) and *Carollia perspicillata*.

Our observations from Nuevo San Juan appear to be the first Amazonian records of diurnal refugia for *Lampronycteris brachyotis*, but extralimital observations (from Central America, Trinidad, and Venezuela; Goodwin and Greenhall, 1961; Handley, 1976; Weinbeer and Kalko, 2004) also suggest that, in caveless landscapes, this species roosts in hollow standing trees.

Genus *Micronycteris* Gray, 1866

The genus *Micronycteris* (sensu stricto; Simmons and Voss, 1998) includes 13 species distinguished from members of other phyllostomid genera by having large, rounded ears connected by a transverse band of skin across the crown of the head, bicolored dorsal fur, unicolored ventral fur, two dermal pads with smoothly rounded lateral margins on the chin, and outer upper incisor and canine always in contact (Simmons, 1996; Williams and Genoways, 2008; Siles et al., 2013; López-Baucells et al., 2018; Siles and Baker, 2020). The taxonomy and systematics of *Micronycteris* has been reviewed by Andersen (1906a), Sanborn (1949a), Simmons (1996), Simmons and Voss (1998), Fonseca et al. (2007), Porter et al. (2007), Larsen et al. (2011), Siles et al. (2013), and Siles and Baker (2020). In their recent revision, Siles and Baker (2020) recognized two dark-bellied subgenera (*Micronycteris* and *Xenoctenes*) and two pale-bellied subgenera (*Leuconycteris* and *Schizonycteris*). We recorded all six species of the genus *Micronycteris* that are expected to occur in the Yavarí-Ucayali interfluve, including members of all four subgenera. Five species occur sympatrically at Nuevo San Juan (*M. hirsuta*, *M. matses*, *M. megalotis*, *M. microtis*, and *M. minuta*).

Micronycteris (*Leuconycteris*) *brosseti* Simmons and Voss, 1998

Voucher material (total = 4): Jenaro Herrera (MUSM 5528), Quebrada Esperanza (FMNH 89100–89102); see table 27 for measurements.

Unvouchered observations: None.

Identification: Siles and Baker (2020) provided a revised diagnosis for the subgenus *Leuconycteris*, which contains only two species, *Micronycteris brosseti* and *M. schmidtorum*. *Micronycteris brosseti* is an Amazonian species that is definitely known from just five localities, two of which are in the Yavarí-Ucayali inter-

TABLE 27

External and Craniodental Measurements (mm) and Weights (g) of *Micronycteris brosseti* and *M. matses* from the Yavarí-Ucayali Interfluve

	M. brosseti		*M. matses*	
	Males[a]	FMNH 89100 ♀	Males[b]	Females[c]
W	5.0	—	9.8 (8.6–10.7) 3	11.6 (10.1–14.0) 5
ToL	57.3 (56–58) 3	58	67.7 (66–69) 3	67.4 (66–69) 5
LT	11.0 (10–13) 3	10	15.0 (14–16) 3	15.0 (13–17) 5
HF	9.3 (8–10) 3	10	11.3 (11–12) 3	11.4 (11–12) 5
E	18.7 (18–19) 3	19	22.3 (21–23) 3	22.4 (22–23) 5
F	31.9 (31.6–32.0) 3	32.8	38.0 (38.0–38.0) 3	38.8 (38.0–40.0) 5
GLS	17.5 (17.4–17.6) 2	17.6	20.1 (19.9–20.3) 3	20.1 (19.8–20.8) 5
CIL	15.7 (15.7–15.8) 2	—	18.5 (18.3–18.6) 3	18.5 (18.3–18.8) 5
PB	3.9 (3.7–4.0) 3	3.9	4.4 (4.3–4.4) 3	4.5 (4.3–4.7) 5
BB	7.2 (7.1–7.3) 3	7.5	8.1 (8.1–8.2) 3	8.2 (7.9–8.4) 5
MB	8.0 (7.8– 8.2) 2	—	9.2 (9.0–9.4) 3	9.2 (8.9–9.4) 5
ZB	8.6 (8.5–8.7) 3	—	9.9 (9.8–10.1) 3	10.0 (9.9–10.2) 5
MTL	6.5 (6.5–6.6) 3	6.6	8.1 (8.0–8.1) 3	8.0 (7.8–8.1) 5
BAM	5.7 (5.5–5.8) 3	5.8	6.7 (6.7–6.8) 3	6.6 (6.4–6.7) 5
BAC	3.0 (3.0–3.1) 3	3.1	3.7 (3.7–3.8) 3	3.6 (3.4–3.7) 5

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 89101, 89102; MUSM 5528.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272814, 273133; MUSM 15231.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273043, 273044, 273095, 273196; MUSM 15229.

fluve.[8] Descriptions and measurements of *M. brosseti* were provided by Simmons and Voss (1998) and Lim et al. (1999). This species is distinguished from other congeners by its small size (e.g., forearm 31–34 mm) and by having pale-gray or buff ventral fur, short (≤4 mm) fur on the leading edge of the pinna, wing digit IV with a second phalange that is shorter than the first phalange, a short tibia (<14.5 mm), and a calcar that is longer than the foot (Simmons and Voss, 1998; López-Baucells et al., 2018). No subspecies are currently recognized (Simmons and Voss, 1998; Williams and Genoways, 2008).

[8] The identification of an Atlantic Forest specimen (from São Paulo; FMNH 92997) previously referred to *Micronycteris brosseti* by Simmons and Voss (1998) is thought to be questionable (Garbino, 2016).

The specimen of *Micronycteris brosseti* from Jenaro Herrera was identified as *M. schmidtorum* by Ascorra et al. (1991a) and Ascorra et al. (1993). This specimen, along with the specimens from Quebrada Esperanza, were subsequently included as "referred material" in the original description of *M. brosseti* by Simmons and Voss (1998: 64–65).

Remarks: According to Ascorra et al. (1991a), the specimen from Jenaro Herrera was mistnetted in secondary vegetation, but whether it was taken in a ground-level or elevated net is unknown. No capture information accompanies the series from Quebrada Esperanza, which was collected in 1957 by C. Kalinowski, probably from a roost.

Micronycteris (*Micronycteris*) *matses*
Simmons et al., 2002

VOUCHER MATERIAL (TOTAL = 9): Nuevo San Juan (AMNH 272814, 273043, 273044, 273095, 273133, 273196; MUSM 15229, 15231), Quebrada Pantaleón (MUSA 15251); see table 27 for measurements.

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: *Micronycteris matses* is only known from the Yavarí-Ucayali interfluve, although it is probably more widely distributed in western Amazonia (Simmons et al., 2002; Medina et al, 2015). This species can be distinguished from other congeners by the following combination of characteristics: dark-brown dorsal and ventral fur, ears connected across the crown by a low interauricular band of skin with a shallow midline notch, short (≤3 mm) fur on the leading edge of the pinna, forearm 38–40 mm, greatest length of skull 19.8–20.8 mm, and lower incisors broad and low crowned (table 27; Simmons et al., 2002). Descriptions and measurements of *M. matses* were provided by Simmons et al. (2002) and Medina et al. (2015). No subspecies are currently recognized (Simmons et al., 2002; Williams and Genoways, 2008).

Specimens of *Micronycteris matses* from Nuevo San Juan were identified as *Micronycteris* "new species" by Fleck et al. (2002). Medina et al. (2015) correctly identified the specimen from Quebrada Pantaleón as *M. matses*.

REMARKS: We mistnetted one specimen of *Micronycteris matses* in the understory of upland primary forest near Nuevo San Juan, but the other seven specimens from this locality were taken at roosts. We found four roosting groups here, all of which occupied deep holes in the sides of dry gullies in primary forest (Simmons et al., 2002). These holes were either old armadillo (*Dasypus pastasae*) burrows, or cavities resulting from soil erosion (but perhaps originally excavated by armadillos). The first of these roosts, encountered on 4 September 1999, was in hillside forest and contained an unknown number of bats; two adult female *M. matses* were collected here, together with specimens of *Peropteryx pallidoptera* and *Carollia brevicauda*. The second roost, encountered on 16 September 1999, also in hillside forest, contained five individuals, of which one adult female was collected. The third roost, encountered on 6 October 1999, was in floodplain forest and contained many bats, of which only one adult male and one adult female *Micronycteris matses* were collected. The fourth roost, encountered on 9 November 1999, was in upland forest and contained seven individuals, of which one adult male and one adult female were collected.

Micronycteris (*Micronycteris*) *megalotis*
(Gray, 1842)

Figure 15A

VOUCHER MATERIAL (TOTAL = 7): Jenaro Herrera (MUSM 5913), Nuevo San Juan (AMNH 273117; MUSM 15217), Quebrada Blanco (MUSM 21192), Quebrada Esperanza (FMNH 89097–89099); see table 28 for measurements.

UNVOUCHERED OBSERVATIONS: None.

IDENTIFICATION: As currently understood *Micronycteris megalotis* is a widespread species that occurs throughout most of the rainforested Neotropical lowlands (Williams and Genoways, 2008). This species can be distinguished from other congeners by the following combination of characteristics: ear length >22 mm; ears connected across the crown by a low interauricular band of skin with a shallow midline notch; fur on lower third of leading edge of pinna 4.5–10 mm in length; white bases of the dorsal hairs between the shoulders approximately one-fourth to one-half the length of each hair; dorsal fur between the shoulders 8–18 mm in length; calcar longer than foot; forearm <36 mm; first and second upper premolars subequal in anteroposterior length; height of first upper premolar very slightly less than that of second upper premolar; and first, second, and third lower premolars similar in size and height (Simmons, 1996; Simmons and Voss, 1998; Simmons et al., 2002; Moras et

FIG. 15. Photographs of **A,** an adult *Micronycteris megalotis* and **B,** an adult *M. hirsuta*, both captured at Jenaro Herrera. Photographs by Marco Tschapka.

TABLE 28

External and Craniodental Measurements (mm) and Weights (g) of *Micronycteris megalotis* and *M. microtis* from the Yavarí-Ucayali Interfluve

	M. megalotis		*M. microtis*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	6.0 (5.6–6.3) 3	–, 7.0	6.8 (5.7–7.5) 15	7.5 (6.6–9.3) 12
ToL	60.6 (59–63) 5	65, 56	60.9 (58–64) 15	62.0 (57–69) 11
LT	13.0 (12–14) 5	14, 9	12.5 (10–14) 15	12.9 (10–15) 11
HF	9.8 (9–11) 5	9, 9	10.6 (10–12) 15	10.3 (9–11) 12
E	21.6 (21–22) 5	22, 19	20.7 (20–21) 15	20.8 (20–22) 12
F	33.9 (33.0–35.0) 5	36.0, 34.5	34.6 (33.0–36.0) 15	35.5 (34.0–37.0) 11
GLS	17.7 (17.1–18.4) 4	17.7, 18.8	18.1 (17.7–18.2) 5	18.1 (17.7–18.4) 3
CIL	16.0 (15.6–16.6) 3	15.9, 17.0	16.3 (16.1–16.7) 5	16.6 (16.3–16.8) 3
PB	3.8 (3.5–4.1) 5	3.7, 4.3	4.0 (3.9–4.2) 5	4.0 (3.9–4.1) 3
BB	7.4 (7.2–7.5) 4	7.2, 7.7	7.5 (7.4–7.6) 5	7.5 (7.3–7.7) 2
MB	8.2 (8.0–8.3) 2	–, 8.5	8.3 (8.1–8.5) 5	8.4 (8.2–8.5) 3
ZB	8.6 (8.4–8.8) 4	–, 9.4	8.9 (8.6–9.3) 5	9.0 (8.9–9.1) 3
MTL	6.8 (6.6–7.1) 5	6.8, 7.2	7.1 (7.0–7.3) 5	7.1 (7.0–7.2) 3
BAM	5.7 (5.6–5.8) 5	5.8, 6.2	5.7 (5.1–6.1) 5	6.0 (6.0–6.1) 3
BAC	3.1 (2.9–3.4) 5	3.1, 3.6	3.2 (3.1–3.3) 5	3.2 (3.1–3.3) 3

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273117; FMNH 89097, 89098; MUSM 15217, 21192.
[b] FMNH 89099; MUSM 5913.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273081, 273098, 273148, 273149, 273169, 273170, 273190, 273192; MUSM 13211, 15218, 15219, 15221, 15224, 15230, 15233.
[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272856, 273072, 273123, 273134, 273163; MUSM 13210, 13212, 15220, 15223, 15225, 15226, 15232.

al., 2015). Descriptions and measurements of *M. megalotis* have been provided by Sanborn (1949a), Goodwin and Greenhall (1961), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons (1996), Simmons and Voss (1998), Simmons et al. (2002), Lim et al. (2005), Fonseca et al. (2007), Larsen et al. (2011), and Moras et al. (2015).

No subspecies are currently recognized (Williams and Genoways, 2008), but recent molecular studies based on one or two markers have suggested that *Micronycteris megalotis* might be a species complex (Clare et al., 2011; Larsen et al., 2011; Siles et al., 2013). However, these studies have not been conclusive and potential species (or subspecies) limits within the complex have not been sufficiently investigated nor documented. Pending more comprehensive studies including larger sample sizes and data from additional molecular markers, we recommend against formally recognizing subspecies of *M. megalotis*.

The voucher material we examined from the Yavarí-Ucayali interfluve was correctly identified as *Micronycteris megalotis* by Simmons (1996), Fleck et al. (2002), Simmons et al. (2002), and Moras et al. (2015). These specimens conform to previous descriptions of *M. megalotis*, and they have measurements that fall within the range of size variation previously documented for the species.

Remarks: Both specimens of *Micronycteris megalotis* from Nuevo San Juan were collected from a single roost inside a very large hollow

standing tree. When this tree was first visited on 18 September 1999 it contained several bats roosting about 4 m above the ground, of which one adult male was collected; several days later (25 September 1999) this roost contained five individuals, of which an additional adult male was collected. No other species appeared to be roosting with *M. megalotis* on either visit.

Bats identified in the literature as *Micronycteris megalotis* have often been reported to roost in hollow trees, but also in a wide variety of other situations; the species is perhaps best considered a roost generalist (Voss et al., 2016).

Micronycteris (*Micronycteris*) *microtis* Miller, 1898

Voucher material (total = 28): Nuevo San Juan (AMNH 272856, 273072, 273081, 273098, 273123, 273134, 273148, 273149, 273163, 273169, 273170, 273190, 273192; MUSM 13210–13212, 15218–15226, 15230, 15232, 15233); see table 28 for measurements.

Unvouchered observations: None.

Identification: *Micronycteris microtis* is widely distributed from southern Mexico to northern Argentina (Williams and Genoways, 2008; Díaz and Barquez, 2009; Reid, 2009; Moras et al., 2015). Our material represents the first record of this species in Peru. *Micronycteris microtis* can be distinguished from other congeners by external and craniodental features including: ear <22 mm; fur on lower third of leading edge of pinna ≤8 mm in length; dorsal fur between the shoulders <11.5 mm in length; calcar longer than foot; forearm <36.5 mm; first and second upper premolars subequal in anteroposterior length; height of first upper premolar very slightly less than that of second upper premolar; and first, second, and third lower premolars similar in size (Simmons and Voss, 1998; Moras et al., 2015). Descriptions and measurements of *M. microtis* have been provided by Brosset and Charles-Dominique (1990), Simmons (1996), Simmons and Voss (1998), Lim et al. (1999), Larsen et al. (2011), and Moras et al. (2015). Two subspecies are currently recognized: *M. m. mexicana* (Mexico to western Costa Rica) and *M. m. microtis* (eastern Nicaragua to South America) (Simmons, 1996).

Fleck et al. (2002) and Moras et al. (2015) correctly identified their material from Nuevo San Juan, which conforms to previous descriptions of *Micronycteris microtis* and has measurements that fall within the previously documented range of size variation for the species. However, one individual from this series (AMNH 273169), which has a cytochrome *b* genetic distance of 4.7% from Brazilian samples of *M. microtis*, was identified as "*M.* sp." by Porter et al. (2007), as "*M.* sp." and *M. megalotis* by Larsen et al. (2011), and as *M. microtis* and "*M.* sp." by Siles et al. (2013). These taxonomic discrepancies reflect ongoing uncertainty about species limits among the dark-bellied forms of *Micronycteris*. Pending resolution of these issues with more extensive sampling and additional molecular markers we recognize the Nuevo San Juan material as *M. microtis* based on the phenotypic data at hand.

Remarks: We captured one individual of *Micronycteris microtis* in a ground-level mistnet in secondary vegetation near Nuevo San Juan, but the 27 other specimens from this locality were taken from roosts (table 29). Most roosts were in tunnellike shelters (hollow logs or animal burrows), but occasionally also in cavities in standing trees; all roosts were found at or near ground level. Most roosts were in well-drained primary upland forest (typically on hill slopes or hillcrests), but one was in secondary vegetation in an old blowdown. *Micronycteris microtis* was usually found roosting alone, but one roost was shared with *M. hirsuta*, and five roosts were shared with *Carollia brevicauda*.

Hollow logs are the commonest roost type from which this species has been reported at Amazonian localities (Voss et al., 2016).

Micronycteris (*Schizonycteris*) *minuta* (Gervais, 1856)

Voucher material (total = 5): Isla Muyuy (MUSM 21196), Nuevo San Juan (AMNH 273172, 273173; MUSM 15227, 15228); see table 30 for measurements.

TABLE 29

Roosting Groups of *Micronycteris microtis* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
25 Jun 1998	cavity in fallen tree	7	no	1 ad. female
8 Jul 1998	cavity in fallen tree	2	yes	2 ad. females
9 Sep 1999	cavity in fallen tree	5	no	1 ad. female
11 Sep 1999	cavity in fallen tree	2	no	1 ad. male
17 Sep 1999	cavity in fallen tree	6	no	1 ad. male
29 Sep 1999	cavity in standing tree	4	no	1 ad. female
6 Oct 1999	animal burrow/hole	"many"	no	1 ad. female
14 Oct 1999	cavity in fallen tree	3	no	1 ad. female, 1 juv. female
14 Oct 1999	cavity in fallen tree	3	yes	2 ad. males, 1 ad. female
20 Oct 1999	animal burrow/hole	2	yes	1 ad. male, 1 ad. female
22 Oct 1999	cavity in fallen tree	unknown	unknown	3 ad. males
23 Oct 1999	animal burrow/hole	"many"	no	1 ad. female
26 Oct 1999	animal burrow/hole	unknown	unknown	1 ad. female, 1 juv. (sex unknown)
4 Nov 1999	cavity in standing tree	4	no	1 ad. male
5 Nov 1999	animal burrow/hole	unknown	unknown	1 ad. male
9 Nov 1999	cavity in fallen tree	5	no	2 ad. males, 1 ad. female, 1 juv. female
11 Nov 1999	cavity in fallen tree	unknown	unknown	1 ad. male, 1 ad. female

Unvouchered observations: None.

Identification: *Micronycteris minuta* is widely distributed from Central America to northern Bolivia and eastern Brazil (Williams and Genoways, 2008; Reid, 2009; Siles and Baker, 2020), but there has been considerable controversy regarding the content of this species over the last two decades (Simmons and Voss, 1998; Lim and Engstrom, 2001a; Ochoa-G. and Sánchez, 2005; Siles and Baker, 2020). *Micronycteris homezorum* (originally named *M. megalotis homezi*; Solari, 2008) was described by Pirlot (1967) based on three specimens from the state of Zulia, Venezuela; unfortunately, the type series was destroyed along with other Pirlot specimens sometime in the 1970s (Simmons and Voss, 1998). Simmons and Voss (1998) elevated *M. homezorum* from subspecies to full species based on a male specimen from French Guiana that exhibited the characteristic cutaneous fossa on the head described by Pirlot (1967). Lim and Engstrom (2001a) subsequently reported a high level of variability among specimens from Guyana in the diagnostic characteristics alleged to differentiate *M. minuta* from *M. homezorum*. After reviewing the morphology of a large series of Venezuelan specimens assignable to either *M. minuta* or *M. homezorum*, Ochoa-G. and Sánchez (2005) concluded that the cutaneous fossa is sexually dimorphic (well developed only in mature males) and is not taxonomically diagnostic; therefore, *M. homezorum* should be regarded as a junior synonym of *M. minuta*. Given that there are no other morphological traits that unambiguously distinguish these taxa, we follow their recommendation here.

Nevertheless, several subsequent molecular studies have suggested that *Micronycteris minuta* is a complex of at least three and perhaps as many as five species (Porter et al., 2007; Clare et al., 2011; Larsen et al., 2011; Siles et al., 2013). Most recently, Siles and Baker (2020) described

TABLE 30

External and Craniodental Measurements (mm) and Weights (g) of *Micronycteris minuta* and *M. hirsuta* from the Yavarí-Ucayali Interfluve

	M. minuta		*M. hirsuta*	
	Males[a]	Females[b]	AMNH 273153 ♂	Females[c]
W	7.7, 6.4	8.9 (7.9–9.5) 3	16.5	15.6 (13.0–18.4) 4
ToL	59, 59	60.0 (59–61) 3	77	77.8 (75–84) 4
LT	13, 12	13.0 (12–14) 3	15	16.5 (14–19) 4
HF	12, 10	12.0 (12–12) 3	13	13.0 (13–13) 4
E	22, 21	21.7 (21–22) 3	26	25.5 (24–26) 4
F	35.0, 35.9	36.0 (36.0–36.0) 3	46.0	45.0 (44.0–46.0) 4
GLS	–, 18.8	—	23.2	22.9 (22.5–23.4) 4
CIL	–, 17.0	—	21.0	20.8 (20.6–21.0) 4
PB	–, 4.1	—	4.8	4.9 (4.8–5.0) 3
BB	–, 7.7	—	8.4	8.6 (8.4–8.7) 3
MB	–, 9.0	—	9.8	10.1 (10.0–10.3) 3
ZB	–, 8.7	—	11.8	11.7 (11.5–12.1) 3
MTL	–, 6.7	—	9.1	9.0 (8.9–9.1) 4
BAM	–, 5.9	—	7.2	7.2 (6.8–7.6) 4
BAC	–, 3.2	—	4.1	4.4 (4.1–4.5) 4

[a] MUSM 15227, 21196.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273172, 273173; MUSM 15228.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 15213, 15214, 15216; ROM 122114.

two new species from this complex, *Micronycteris tresamici* (from Honduras and Costa Rica) and *M. simmonsae* (from eastern Ecuador). Those authors applied the name *M. minuta* to samples from Panama southward through northern South America, western Ecuador, Peru, Bolivia, and Brazil; however, they suggested that *M. minuta* (thus restricted) may still be a complex of more than one species. In the absence of denser geographic sampling of South American populations and molecular data from topotypic specimens of *minuta* (with type locality at Capella-Nova, Minas Gerais, Brazil), *homezorum* (with type locality fixed by neotype selection as Hato El Cedral, Apure, Venezuela; Ochoa-G. and Sánchez, 2005), and *hypoleuca* Allen, 1900 (with type locality Bonda, Magdalena, Colombia), it is not yet possible to determine whether additional genetic lineages in this complex are distinct taxa, nor to decide which names apply to them. For now, we follow Siles and Baker (2020) and treat these nominal taxa as conspecific.

As thus defined, *Micronycteris minuta* is distinguished from other congeners by the following characteristics: dark-brown dorsal fur and pale (gray or buff) ventral fur; a cutaneous fossa on the top of the head in mature males; calcar shorter than foot; zygomatic breadth greater than breadth of braincase, but less than mastoid breadth; sagittal crest absent or present only on the anteriormost third to two-thirds of the parietals; upper incisors bilobed; M1 narrower than M2 in occlusal view; lower incisors bilobed; first lower premolar slightly larger and taller than third lower premolar; and second lower premolar reduced, shorter than first and third lower

premolars (Ochoa-G. and Sánchez, 2005; Williams and Genoways, 2008; Siles and Baker, 2020). Descriptions and measurements of *Micronycteris minuta* were provided by Simmons and Voss (1998), Bernard (2001), Lim and Engstrom (2001a), Ochoa-G. and Sánchez (2005), Siles et al. (2013), and Siles and Baker (2020).[9] We follow Williams and Genoways (2008) and Siles and Baker (2020) in not recognizing subspecies of *Micronycteris minuta* due to the taxonomic uncertainties described above.

Fleck et al. (2002) correctly identified their material from Nuevo San Juan as *Micronycteris minuta*, but one individual from this series (AMNH 273172) was subsequently identified as *M.* cf. *schmidtorum* by Larsen et al. (2011), as *M. schmidtorum* by Siles et al. (2013) and, finally, as *M. minuta* again by Siles and Baker (2020). Our material from the Yavarí-Ucayali interfluve conforms to previous descriptions of *M. minuta*, with measurements that fall within the range of size variation previously documented for the species. However, a cytochrome *b* sequence from AMNH 273172 is 4.4% divergent from both a Bolivian clade of *M. minuta* and a second clade encompassing Brazilian and northern South American sequences (Siles and Baker, 2020). Therefore, it is possible that the population in the Yavarí-Ucayali interfluve may eventually be shown to represent a distinct taxon and require another name if *M. minuta* is further subdivided.

Remarks: All our specimens of *Micronycteris minuta* from Nuevo San Juan were collected from a single roost, where about 17 individuals were clustered approximately 4 m above the ground inside a hollow standing tree in primary hillside forest; of these, one adult male and three adult females were collected on 23 October 1999. No other bat species were observed in this roost.

Other members of the *Micronycteris minuta* complex are also known to roost in hollow standing trees (Goodwin and Greenhall, 1961; Handley, 1976; Rengifo et al., 2013).

[9] But note that some authors measured specimens that are now treated as distinct species (i.e., *M. tresamici* and *M. simmonsae*).

Micronycteris (*Xenoctenes*) *hirsuta*
(Peters, 1869)

Figure 15B

Voucher material (total = 6): Jenaro Herrera (ROM 122114); Nuevo San Juan (AMNH 273153; MUSM 15213–15216); see table 30 for measurements.

Unvouchered observations: None.

Identification: *Micronycteris hirsuta* is a widespread species that occurs from southern Honduras to northern South America, with a disjunct population in southeastern Brazil (Williams and Genoways, 2008; Reid, 2009). *Micronycteris hirsuta* is easily distinguished from other congeneric species by its large size (forearm >40 mm, greatest length of skull >21 mm), and uniquely high-crowned but mesiodistally narrow lower incisors (Simmons et al., 2002: fig. 3B; López-Baucells et al., 2018). Descriptions and measurements of *M. hirsuta* were provided by Andersen (1906a), Sanborn (1949a), Goodwin and Greenhall (1961), Swanepoel and Genoways (1979), Genoways et al. (1981), Brosset and Charles-Dominique (1990), Simmons (1996), Simmons and Voss (1998), Simmons et al. (2002), Lim et al. (2005), Fonseca et al. (2007), and Larsen et al. (2011). No subspecies are currently recognized, but a revision of the species is needed (Williams and Genoways, 2008).

Fleck et al. (2002), Simmons et al. (2002), and Larsen et al. (2011) correctly identified the specimens from Nuevo San Juan as *Micronycteris hirsuta*. Voucher material from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, and measurements fall within the previously documented range of intraspecific size variation.

Remarks: One individual of *Micronycteris hirsuta* was taken in a ground-level mistnet in secondary vegetation at Jenaro Herrera on 17 January 2012, but the other specimens captured in our region were taken at roosts. We found three roosts of this species near Nuevo San Juan. The first, encountered on 13 October 1999, was a hollow standing tree at the edge of

an abandoned Matses swidden; two individuals (of which one adult female was collected) were roosting about 2 m above ground level in the dark interior. The second roost, encountered on 15 October 1999, was a hollow standing tree in primary hilltop forest; three individuals (one adult male, one adult female, and one juvenile male) were roosting 4 m above the ground in the dark interior. The third roost, encountered on 20 October 1999, was a hole in the side of a stream headwater gully, about 1 m in diameter and too deep for the end to be visible; one adult female *M. hirsuta* and two individuals of *M. microtis* were collected here.

Most roosts of *Micronycteris hirsuta* previously reported in the literature have been discovered inside hollow trees (Goodwin and Greenhall, 1961; Tuttle, 1970; Simmons and Voss, 1998).

Subfamily Phyllostominae Gray, 1825

The subfamily Phyllostominae currently includes 23 species in 10 genera (*Chrotopterus*, *Gardnerycteris*, *Lophostoma*, *Macrophyllum*, *Mimon*, *Phylloderma*, *Phyllostomus*, *Tonatia*, *Trachops*, and *Vampyrum*) (Dávalos et al., 2014; Baker et al., 2016; Cirranello et al., 2016; Rojas et al., 2016; Simmons and Cirranello, 2020). Historically, this subfamily was defined more broadly to include all the insectivorous/animalivorous phyllostomids, including taxa now classified in Macrotinae, Micronycterinae, Lonchorhininae, and Glyphonycterinae (Wetterer et al., 2000; Williams and Genoways, 2008). However, analyses of molecular data have convincingly demonstrated that genera now included in those subfamilies do not form a clade with Phyllostominae *sensu stricto* (Baker et al., 2003; Baker et al., 2016). Phyllostomines are characterized by having a noseleaf with a spear that is equal to or longer than twice the height of the horseshoe; a noseleaf rib that extends all the way to the apex of the spear; a single interramal vibrissa; pinnae with smoothly rounded (not concave) lateral margins; wing digit IV with subequal first and second phalanges; and outer upper incisors that are always in contact with the canines (Cirranello et al., 2016). We recorded all 13 phyllostomine species with geographic ranges that overlap the Yavarí-Ucayali interfluve.

Chrotopterus auritus (Peters, 1856)

Figure 16A

Voucher material (total = 3): Jenaro Herrera (MUSM 5506), Nuevo San Juan (AMNH 272843; MUSM 13196); see table 31 for measurements.

Unvouchered observations: One individual of *Chrotopterus auritus* was captured at Divisor during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006).

Identification: *Chrotopterus* is a widespread, monotypic genus that ranges from southern Mexico to northern Argentina (Medellín, 1989; Williams and Genoways, 2008). It is easily distinguished from other phyllostomines by the following characteristics: large size (forearm 74–83 mm, greatest length of skull 34–37 mm), lower portion of noseleaf cup shaped, pelage long and woolly, tail rudimentary, calcar longer than foot, wing tips whitish, and lower incisor series reduced to a single tooth on each side (Medellín, 1989; Williams and Genoways, 2008; López-Baucells et al., 2018). Descriptions and measurements of *Chrotopterus auritus* were provided by Thomas (1905), Taddei (1975), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Medellín (1989), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Wetterer et al. (2000), Lim et al. (2005), and Williams and Genoways (2008).

Three subspecies have been recognized: *Chrotopterus auritus auritus* (Mexico to Panama and western Colombia, Ecuador, and Peru), *C. a. australis* (southeastern Peru, Bolivia, southern Brazil, Paraguay, and northern Argentina), and *C. a. guianae* (eastern Colombia, Venezuela, the Guianas, and northern Brazil) (Thomas,

FIG. 16. Photographs of **A,** an adult *Chrotopterus auritus* captured at Quebrada Blanco and **B,** an adult female (ROM 122118) *Gardnerycteris crenulata* captured at Jenaro Herrera. Photographs by Marco Tschapka (A) and Burton Lim (B).

TABLE 31

External and Craniodental Measurements (mm) and Weights (g) of *Chrotopterus auritus* and *Gardnerycteris crenulata* from the Yavarí-Ucayali Interfluve

	C. auritus	*G. crenulata*	
	Males[a]	Males[b]	Females[c]
W	65.7 (62.0–68.0) 3	13.8 (12.0–21.0) 9	14.1 (12.5–15.0) 6
ToL	117.7 (112–121) 3	82.3 (75–92) 9	87.0 (77–93) 10
LT	14.7 (10–22) 3	22.9 (20–27) 9	23.1 (21–27) 10
HF	23.7 (20–26) 3	11.2 (9.5–13.0) 10	11.4 (9.9–13.0) 11
E	44.7 (44–45) 3	23.7 (22–26) 9	24.4 (23–26) 10
F	80.0 (78.0–81.0) 3	48.0 (45.3–50.0) 10	48.5 (43.0–51.0) 11
GLS	34.5 (34.1–35.2) 3	21.4 (21.0–21.8) 5	21.4 (21.0–22.2) 5
CIL	30.7 (30.4–30.8) 3	19.4 (19.1–20.0) 5	19.5 (18.8–20.3) 5
PB	6.1 (5.9–6.2) 3	4.1 (3.9–4.3) 5	4.2 (3.8–4.5) 5
BB	13.3 (13.0–13.6) 3	8.4 (8.1–8.8) 5	8.5 (8.2–8.6) 4
MB	16.6 (16.5–16.8) 3	11.3 (11.0–11.6) 5	11.3 (11.0–11.6) 5
ZB	18.8 (18.2–19.3) 3	12.0 (11.5–12.4) 5	12.1 (11.4–12.3) 5
MTL	13.0 (12.7–13.1) 3	7.9 (7.8–8.1) 5	7.9 (7.6–8.2) 5
BAM	12.0 (11.5–12.6) 3	8.4 (8.1–8.6) 5	8.5 (8.0–8.8) 5
BAC	7.7 (7.3–8.2) 3	5.4 (5.2–5.5) 5	5.4 (5.2–5.6) 5

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272843; MUSM 5506, 13196.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272770; CEBIOMAS 105; FMNH 89151; MUSM 869, 5914, 13215, 13217, 21198, 32052, 32054.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272769, 272834, 278488; FMNH 89038–89040, 89152; MUSM 870, 13216, 32053, 32055.

1905; Cabrera, 1958; Jones and Carter, 1976; Medellín, 1989). However, many recent authors have noted that patterns of morphological variation in *C. auritus* do not conform to this arrangement and that no subspecific classification is warranted (Handley, 1966; Koopman, 1994; Simmons and Voss, 1998; Williams and Genoways, 2008). More recently, Clare (2011) and Clare et al. (2011) explored the genetic diversity in *C. auritus* using the mitochondrial COI gene and an intron region of the Dby gene in a limited geographical sample. They found evidence that *C. auritus* might be a species complex including as many as three taxa, but until more geographically comprehensive multigene studies are completed, we recommend against recognizing subspecies of *C. auritus*.

Ascorra et al. (1993) and Fleck et al. (2002) correctly identified their material from Jenaro Herrera and Nuevo San Juan, respectively, as *Chrotopterus auritus*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the previously documented range of size variation for *C. auritus*.

Remarks: No ecological information is available for the specimen of *Chrotopterus auritus* captured at Jenaro Herrera. The specimens from Nuevo San Juan were both captured in ground-level mistnets, the first on 1 July 1998 in closed-canopy secondary vegetation, the second on 6 July 1998 in hillcrest primary forest. No roosting groups of this species were encountered during our study.

Gardnerycteris crenulata
(É. Geoffroy St.-Hilaire, 1803)

Figure 16B

Voucher material (total = 21): Estación Biológica Madre Selva (MUSM 32052–32055), Jenaro Herrera (AMNH 278488; CEBIOMAS 105; MUSM 869, 870, 5914), Nuevo San Juan (AMNH 272769, 272770, 272834; MUSM 13215–13217), Quebrada Blanco (MUSM 21198), San Vicente (FMNH 89038–89040, 89151, 89152); see table 31 for measurements.

Unvouchered observations: An unspecified number of individuals of *Gardnerycteris crenulata* were captured at Anguila during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015). We captured two individuals at Frog Valley on 17 February 2019 and three more individuals at Tahuayo Farm on 19 February 2019. *Gardnerycteris crenulata* was also recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: This species was formerly known as *Mimon crenulatum*, but phylogenetic analyses of molecular sequence data have shown that *Mimon*, as traditionally recognized (e.g., by Simmons and Voss, 1998), was polyphyletic (Dávalos et al., 2012, 2014; Rojas et al., 2016). Because the type species of *Mimon* is *M. bennettii*, and no generic name was available for *M. crenulatum* and *M. koepckeae*, Hurtado and Pacheco (2014) provided a new genus, *Gardnerycteris* (feminine in gender), for these closely related species. Subsequently, Hurtado and D'Elía (2018) completed a review of *Gardnerycteris* based on mitochondrial genes, one nuclear gene, and morphology, and recognized three species: *G. crenulata* (in eastern Venezuela, Trinidad, and the Guianas west into Ecuador, eastern Peru, Bolivia, and Brazil), *G. koepckeae* (in highland areas of Colombia, Peru, and Bolivia [Morales-Martínez et al. 2020; Siles and Wallace, 2021]), and *G. keenani* (in southern Mexico southeastward into northwestern Venezuela, western Colombia, Ecuador, and extreme northwestern Peru).

Gardnerycteris crenulata is distinguished from other congeners by the following combination of traits: dorsal fur short and sparse, with a narrow, whitish (not yellowish) middorsal stripe; noseleaf with lateral hairs evenly distributed and about the same length (without a concentration of longer hairs at the apex); central rib of noseleaf hairless; skin of noseleaf uniformly pigmented (not darker distally); bright and conspicuous whitish auricular patches; ear <22 mm; borders of pinna wrinkled; inner lobe of pinna well developed; metacarpal III longer than metacarpal V; fringe of hairs present on uropatagium; anterior border of nasal bones U-shaped; deep median depression on rostrum; posterior border of braincase tapering, not rounded; high sagittal crest present; hard palate long, with U-shaped posterior border; and absence of a lingual flexus between protocone[10] and hypocone on M1 and M2 (Hurtado et al., 2014; Hurtado and Pacheco, 2014; Hurtado and D'Elía, 2018). Descriptions and measurements of *G. crenulata* have been provided by Handley (1960), Goodwin and Greenhall (1961), Husson (1962, 1978), Hill (1964), Gardner and Patton (1972), Genoways and Williams (1979), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Pedro et al. (1994), Simmons and Voss (1998), Lim et al. (2005), Hurtado et al. (2014), Hurtado and Pacheco (2014), and Hurtado and D'Elía (2018).

Even after the removal of *koepckeae* and *keenani* from the synonymy of *Gardnerycteris crenulata*, several nominal subspecies remain: *G. c. crenulata* (eastern Venezuela, Trinidad, and the Guianas southward into the lower Amazon basin and along the Atlantic Coast of Brazil to Minas Gerais), *G. c. longifolium* (southern Colombia, eastern Ecuador and Peru, western and central Brazil, and northern Bolivia), *G. c. peruanum* (eastern Peru at ca. 1700 m), and *G. c. picatum* (eastern Brazil) (Williams and Genoways, 2008; Tavares et al., 2010; Hurtado and D'Elía, 2018).

[10] Hurtado and D'Elía (2018) incorrectly identified this cusp as the paracone.

In their recent review of the genus, Hurtado and D'Elía (2018) suggested that *peruanum* may actually be associated with *G. koepckeae* rather than with *G. crenulata*, and that *picatum* is best regarded as a junior synonym of *G. c. crenulata*. The nominal subspecies *longifolium* remains problematic: Hurtado and Pacheco (2014) recognized it as a synonym of *G. c. crenulata*, but more recently Hurtado and D'Elía (2018) suggested that the southern populations previously attributed to *longifolium* should be referred to that subspecies, but that more northern forms may represent a distinct subspecies. Pending a complete revision of the subspecies nomenclature for the Peruvian region, we prefer not to refer our material to subspecies.

Ascorra et al. (1993), Fleck et al. (2002), Hurtado and Pacheco (2014), and Hurtado and D'Elía (2018) all correctly identified their specimens from the Yavarí-Ucayali interfluve as *Gardnerycteris crenulata*. Our voucher material conforms to all previous qualitative and morphometric characterizations of the species.

Remarks: Of 34 captures of *Gardnerycteris crenulata* accompanied by ecological data from our region, 30 were made in ground-level mist-nets, 1 was made in an elevated net, and 3 were made in harp traps. Twenty-seven captures were made in primary forest and seven in secondary vegetation. No roosts of this species were encountered during our study.

Genus *Lophostoma* d'Orbigny, 1836

The genus *Lophostoma* includes seven species distinguished from other phyllostomines by the following shared characteristics: very large, rounded ears; chin with a U-shaped row of small tubercles; face sparsely furred with short hairs (muzzle may appear nearly naked); skull with narrow postorbital constriction (<5.5 mm; less than 90% of breadth across cingula of canines); and one incisor and three premolars in each mandible (Williams and Genoways, 2008). With live individuals in hand, species of *Lophostoma* can often be distinguished from superficially similar taxa (e.g., *Tonatia* spp., *Micronycteris* spp.) by touching their ears: species of *Lophostoma* typically fold their ears down over the top of the head when touched, whereas other large-eared phyllostomines do not. The taxonomy and systematics of *Lophostoma* have been reviewed by Davis and Carter (1978), Lee et al. (2002), Porter et al. (2003), Baker et al. (2004), Fonseca and Pinto (2004), Velazco and Cadenillas (2011), Velazco and Gardner (2012), and Camacho et al. (2016). Velazco and Gardner (2012) provided a key to the species, of which we recorded all three that are expected to occur in the Yavarí-Ucayali interfluve.

Lophostoma brasiliense Peters, 1867

Figure 17A

Voucher material (total = 14): Jenaro Herrera (MUSM 5915, 5938), Nuevo San Juan (AMNH 272728–272732; MUSM 13264–13269), Quebrada Lobo (MUSA 15140); see table 32 for measurements.

Unvouchered observations: None.

Identification: *Lophostoma brasiliense* is a widespread species (or species complex; see below) that ranges from southern Mexico to central Bolivia and northeastern Brazil (Williams and Genoways, 2008; Reid, 2009). As currently recognized, this species is easily distinguished from other congeners by its small size (forearm <40 mm, greatest length of skull <22 mm), grayish or brownish (not white or cream) ventral fur, and lack of small warts on the forearm (Reid, 2009; Velazco and Gardner, 2012; López-Baucells et al., 2018). Descriptions and measurements of *L. brasiliense* were provided by Goodwin (1942), Goodwin and Greenhall (1961), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Lim et al. (2005), Regalado and Albuja (2012), Velazco and Cadenillas (2011), and Velazco and Gardner (2012). No subspecies are currently recognized (Williams and Genoways, 2008), but analyses of mitochondrial DNA sequence data suggest that

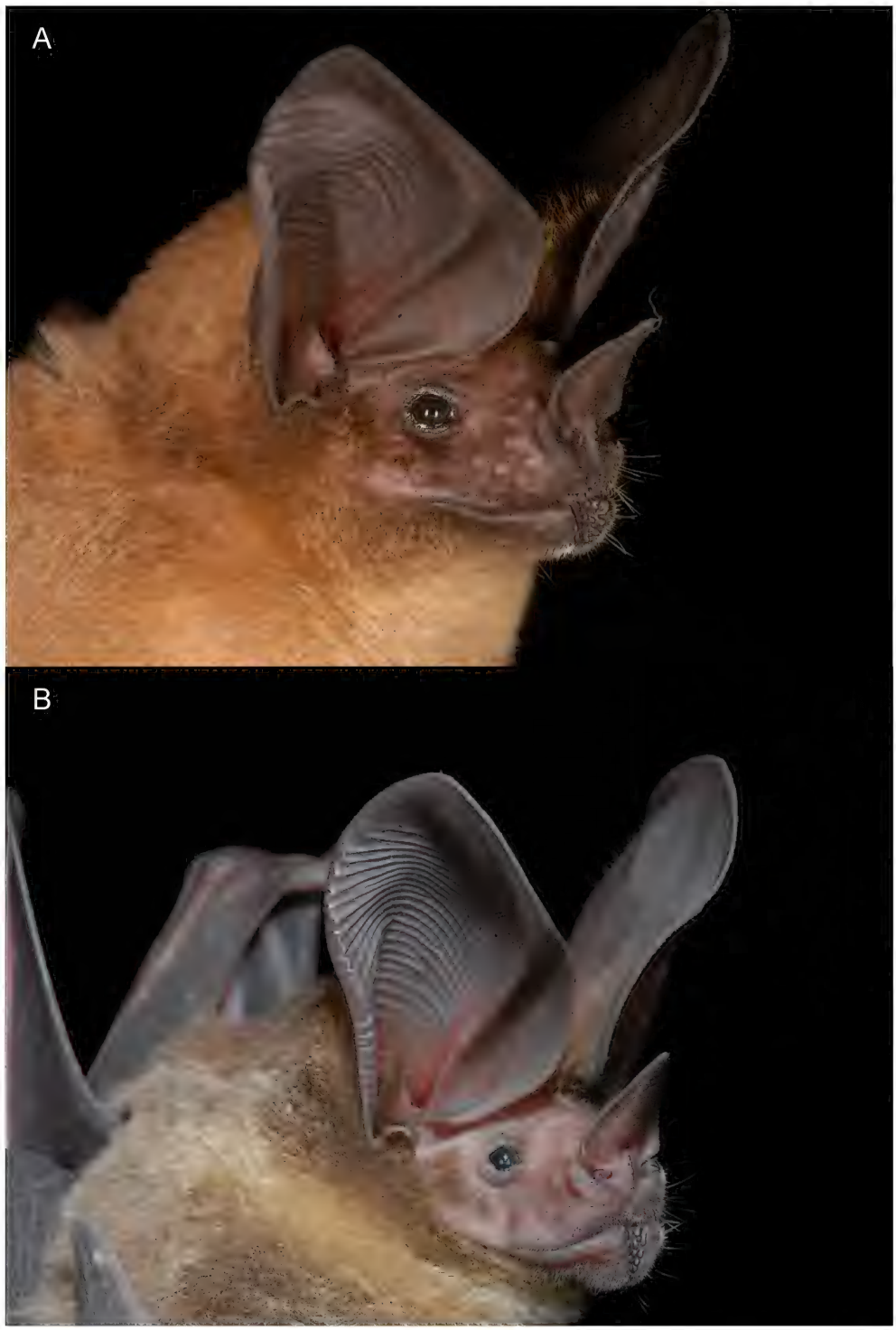


FIG. 17. Photographs of **A,** an adult *Lophostoma brasiliense* captured at Quebrada Blanco; and **B,** an adult female (ROM 122117) *L. silvicolum* captured at Jenaro Herrera. Photographs by Marco Tschapka (A) and Burton Lim (B).

TABLE 32

External and Craniodental Measurements (mm) and Weights (g) of *Lophostoma brasiliense*, *L. carrikeri*, and *L. silvicolum* from the Yavarí-Ucayali Interfluve

	L. brasiliense		*L. carrikeri*	*L. silvicolum*	
	Males[a]	Females[b]	Males[c]	Males[d]	Females[e]
W	9.6 (8.7–10.5) 7	9.4 (8.1–11.0) 6	20.0, 24.0	35.2 (30.0–46.0) 6	28.4 (23.0–33.8) 16
ToL	69.3 (67–72) 7	68.7 (60–73) 6	80, 82	99.8 (94–108) 6	94.3 (82–105) 16
LT	10.7 (8–13) 7	9.5 (8–11) 6	15, 14	19.0 (16–22) 6	17.8 (15–21) 16
HF	11.4 (10–12) 7	11.0 (10–12) 6	13, 12	15.8 (11–18) 6	15.7 (13–18) 16
E	25.3 (24–29) 7	24.5 (24–25) 6	28, 26	36.2 (34–38) 6	35.5 (33–39) 16
F	35.1 (34.0–37.0) 7	34.9 (34.0–35.8) 6	46.2, 45.6	55.9 (55.0–56.2) 6	54.4 (50.6–59.0) 16
GLS	19.3	19.5	23.2, 23.8	27.6 (26.6–28.7) 8	26.5 (25.1–27.5) 15
CIL	17.1	17.1	21.0, 20.5	24.7 (23.8–25.3) 8	23.9 (23.0–24.9) 15
PB	3.2	3.2	3.7, 3.9	4.1 (4.0–4.3) 8	4.0 (3.7–4.3) 15
BB	8.1	8.0	9.6, 9.6	10.5 (10.2–10.8) 7	10.4 (10.1–10.9) 15
MB	9.1	9.0	11.9, 11.9	13.8 (13.4–14.7) 8	13.1 (12.5–13.6) 15
ZB	9.0	9.1	10.9, 11.2	13.7 (13.1–14.5) 7	13.0 (12.1–13.8) 15
MTL	6.7	6.9	8.3, 8.2	10.1 (9.8–10.6) 8	9.7 (9.4–10.1) 15
BAM	5.9	6.1	7.5, 7.5	9.0 (8.7–9.3) 8	8.7 (8.3–9.4) 15
BAC	3.9	3.9	5.0, 4.8	6.3 (6.0–6.7) 8	5.7 (5.3–6.1) 15

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272730–272732; MUSM 5938, 13264, 13267, 13268.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272728, 272729; MUSM 5915, 13265, 13266, 13269.

[c] MUSM 6977, 21175.

[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 73721, 74101, 272829, 272833, 273087; MUSM 13273, 15285, 21176.

[e] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74102, 272746, 272800, 272801, 273074, 278475, 278503; CEBIOMAS 102; MUSM 873, 5937, 13272, 13274–13276, 15284, 21177, 32009.

there might be two evolutionarily distinct lineages of *L. brasiliense*, one in Central America and the other in South America (Clare et al., 2011; Velazco and Cadenillas, 2011). We compared our voucher material from the Yavarí-Ucayali interfluve with other specimens of *L. brasiliense* throughout its distribution and found no morphological variation to warrant the recognition of more than one taxon.

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their specimens from Jenaro Herrera, Nuevo San Juan, and Quebrada Lobo, respectively, as *Lophostoma brasiliense*. Voucher material from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the range of size variation previously documented for *L. brasiliense*.

Remarks: We found a single roost of *Lophostoma brasiliense* near Nuevo San Juan on 14 June 1998, from which all the specimens collected at this locality were taken. The roosting group consisted of 14 or 15 individuals, of which we captured three adult males, four adult females, three immature males, and one immature female (R.S.V. saw only three escape, but the Matses children who watched him extracting bats by hand from this roost said that four got away). The bats occupied a single chamber inside a large, active, arboreal termite nest attached to a

spiny palm (*Astrocaryum* spp.) in dense secondary vegetation. An inconspicuous entrance tunnel about 30 cm long provided access from the underside of the nest, which was about 1.6 m above the ground.

All previously reported roosts of this species have also been found in arboreal termite nests (Goodwin and Greenhall, 1961; Kalko et al., 2006; York et al., 2008; Esquivel et al., 2020).

Lophostoma carrikeri (Allen, 1910)

Voucher material (total = 2): Isla Muyuy (MUSM 21175), Jenaro Herrera (MUSM 6977); see table 32 for measurements.

Unvouchered observations: One individual of *Lophostoma carrikeri* was captured at the Quebrada Buenavista locality during the Yavarí Rapid Biological Inventory (Escobedo, 2003).

Identification: Until quite recently, three species of white-bellied *Lophostoma* were recognized as valid: *L. carrikeri*, *L. kalkoae*, and *L. yasuni* (see Velazco and Gardner, 2012). However, Camacho et al. (2016) examined the holotype and only specimen known of *L. yasuni* using morphological and molecular approaches and concluded that it was conspecific with *L. carrikeri*, and that *yasuni* should thus be regarded as a junior synonym. This species can be distinguished from other members of the genus by the following combination of features: pale to whitish fur on the throat; lack of postauricular patches; proximal one-third of the dorsal surface of forearm sparsely covered by short hairs; deeper basisphenoid pits with septum conspicuously narrower; and presence of a weak indentation on the lingual cingulum of each upper canine (Velazco and Gardner, 2012). Descriptions and measurements of *L. carrikeri* were provided by Allen (1910), Goodwin (1942), Swanepoel and Genoways (1979), Genoways and Williams (1980), Williams and Genoways (1980a), McCarthy et al. (1983), Gribel and Taddei (1989), McCarthy et al. (1992), Simmons and Voss (1998), Lim et al. (1999), Lim et al. (2005), Zortea et al. (2009), Velazco and Cadenillas (2011), Velazco and Gardner (2012), Camacho et al. (2014, 2016), and Brandão et al. (2020). No subspecies are currently recognized (Camacho et al., 2016).

Ascorra et al. (1993) and Velazco and Gardner (2012) correctly identified specimens from the Yavarí-Ucayali interfluve as *Lophostoma carrikeri*. Our voucher material conforms to previous descriptions of the species, with measurements that fall within the range of size variation previously documented for *L. carrikeri*.

Remarks: No definite ecological information accompanies recorded captures of *Lophostoma carrikeri* from our region.

Lophostoma silvicolum d'Orbigny, 1836

Figures 17B, 18

Voucher material (total = 26): Estación Biológica Madre Selva (MUSM 32009), Jenaro Herrera (AMNH 278475, 278503; CEBIOMAS 102; MUSM 873, 5937), Nuevo San Juan (AMNH 272746, 272800, 272801, 272829, 272833, 273074, 273087; MUSM 13272–13276, 15283–15285), Orosa (AMNH 73721, 74101, 74102), Quebrada Blanco (MUSM 21176, 21177); see table 32 for measurements.

Unvouchered observations: One individual of *Lophostoma silvicolum* was captured at Divisor during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006). During the Yavarí Rapid Biological Inventory, one individual of *L. silvicolum* was captured at Quebrada Curacinha, and two others were captured at Quebrada Limera (Escobedo, 2003).

Identification: *Lophostoma silvicolum* is distinguished from other congeners by the following combination of characteristics: large size (forearm >45 mm, greatest length of skull >24 mm), brownish to grayish ventral fur, postauricular patches absent, forearm naked, strong indentation present on the lingual cingulum of each upper canine, M1 hypocone moderately to well developed, and second lower premolar aligned with toothrow in occlusal view (Velazco

FIG. 18. *Lophostoma silvicolum* using an arboreal termite nest as roost at Jenaro Herrera. Photograph by Marco Tschapka.

and Gardner, 2012; López-Baucells et al., 2018). Descriptions and measurements of *L. silvicolum* were provided by Goodwin (1942), Husson (1962, 1978), Davis and Carter (1978), Swanepoel and Genoways (1979), Genoways and Williams (1980), Medellín and Arita (1989), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Baker et al. (2004), Lim et al. (2005), Velazco and Cadenillas (2011), Velazco and Gardner (2012), Smith et al. (2012), and Velazco and Patterson (2019). Three subspecies are currently recognized: *L. s. centralis* (eastern Honduras to Costa Rica), *L. s. laephotis* (Guianas to the lower Amazon basin of Brazil), and *L. s. silvicolum* (Panama southward throughout most of the humid-tropical lowlands of South America) (Williams and Genoways, 2008; Velazco and Cadenillas, 2011).

Velazco and Cadenillas (2011) analyzed cytochrome *b* sequences from all *Lophostoma* species and found that *L. silvicolum* sequences grouped into three clades. *Lophostoma silvicolum* was paraphyletic in their cytochrome *b* tree, with *L. evotis* sister to a clade of *L. silvicolum* that contained specimens from Panama, Venezuela, eastern Ecuador, and eastern Peru. Cytochrome *b* sequence divergence among the various lineages of *L. silvicolum* and *L. evotis* ranged from 3.7 to 6.3%. However, those authors examined approximately 300 specimens of *L. silvicolum* from throughout its distribution and could not find any clear pattern of qualitative-morphological or morphometric variation that matched any of the three molecular clades or any of the traditionally recognized subspecies. Given these findings, we recommend against taxonomic changes (or recognition of subspecies) pending analyses of nuclear markers in this complex.

Ascorra et al. (1993), Fleck et al. (2002), and Velazco and Cadenillas (2011) correctly

identified their specimens from Jenaro Herrera, Nuevo San Juan, Orosa, and Quebrada Blanco as *Lophostoma silvicolum*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, and measurements fall within the range of size variation previously documented for *L. silvicolum*.

Remarks: Of 22 nocturnal captures of *Lophostoma silvicolum* recorded from our region, 21 were in ground-level mistnets; of these, 8 were in primary forest, 12 were in secondary vegetation, and 1 was in a palm swamp (*aguajal*). One additional individual was taken in a banana-baited rat trap tied to a liana about 1 m above the ground in primary forest.

We found four roosts of this species near Nuevo San Juan, all of them in arboreal termite nests. The first roost, about 2 m above the ground in secondary vegetation, contained five or six individuals (of which one adult female was collected on 22 May 1998). The second roost, about 4 m above the ground in secondary vegetation, contained two individuals (an adult female and her nursing offspring, both collected on 9 September 1999). The third roost, about 2.5 m above the ground in primary valley-bottom forest, contained five individuals (of which one adult male and one adult female were collected on 11 September 1999). The fourth roost, about 5 m above the ground in secondary vegetation, contained two individuals (of which one adult male was collected on 23 September 1999). *Lophostoma silvicolum* was usually found roosting without other species of bats, but the second roost described above was shared with a single adult male *Phyllostomus hastatus*.

Lophostoma silvicolum is well known to construct roosts in active termite nests (fig. 18), which are sometimes coinhabited by *Phyllostomus hastatus* (see Tuttle, 1970; Kalko et al., 1999, 2006; Díaz and Linares García, 2012; Rengifo et al., 2013). However, *P. hastatus* seems to be a roost parasite that is not believed to participate in roost construction or maintenance (Kalko et al., 2006).

Macrophyllum macrophyllum (Schinz, 1821)

Voucher material (total = 2): Nuevo San Juan (AMNH 273075; MUSM 15212); see table 33 for measurements.

Unvouchered observations: None.

Identification: *Macrophyllum*, a monotypic genus, is easily distinguished from other phyllostomines by the following combinations of characteristics: relatively small size (7–10 g); a long tail that does not quite reach the outer edge of an extensive uropatagium supported by long calcars; very long feet (≥10 mm); longitudinal rows of denticles on the distal lower surface of the uropatagium; a lanceolate noseleaf with a medial ridge; short rostrum; nares emarginated laterally and dorsally, exposing a flattish area over the incisor roots; two pairs of lower incisors; and second lower premolars minute and crowded lingually, such that the first and third lower premolars are almost in contact (Harrison, 1975; Reid, 2009; López-Baucells et al., 2018). Descriptions and measurements of *M. macrophyllum* were provided by Davis et al. (1964), Hill (1964), Harrison and Pendleton (1974), Harrison (1975), Taddei (1975), Husson (1978), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Barquez et al. (1999), López-Gonzáles (2005), and Feijó et al. (2015). No subspecies are currently recognized (Williams and Genoways, 2008).

Fleck et al. (2002) correctly identified their specimens from Nuevo San Juan, which conform to previous qualitative and morphometric descriptions of *Macrophyllum macrophyllum*.

Remarks: We found a single roosting group of *Macrophyllum macrophyllum* near Nuevo San Juan, consisting of two individuals (both adult males; collected on 10 September 1999) on the underside of a large tree that had fallen across a stream in primary forest. The bats were sheltered in a deep recess between two downward-facing buttresses directly over the water. No other bats were found in this roost.

Most previously described roosts of *Macrophyllum macrophyllum* have been found in caves or

TABLE 33

External and Craniodental Measurements (mm) and Weights (g) of *Macrophyllum macrophyllum*, *Phylloderma stenops*, and *Phyllostomus discolor* from the Yavarí-Ucayali Interfluve

	M. macrophyllum	*Phylloderma stenops*	*Phyllostomus discolor*	
	Males[a]	Males[b]	Males[c]	Females[d]
W	8.9, 8.9	52.3 (50.0–57.0) 3	32.0, 40.0	35.5 (32.0–38.0) 4
ToL	94, 89	112.5 (110–115) 3	92, 97	95.8 (91–100) 4
LT	46, 43	18.7 (16–20) 3	13, 14	13.8 (10–17) 4
HF	13, 13	19.3 (18–20) 3	10, 13	14.5 (14–15) 4
E	20, 17	27.3 (27–28) 3	25, 23	23.8 (22–28) 4
F	37.0, 35.0	73.4 (72.0–75.0) 3	62.5, 61.3	61.9 (59.4–64.2) 4
GLS	16.7, –	30.7 (30.2–31.0) 3	29.0, 28.6	28.8 (28.1–29.9) 4
CIL	15.2, –	28.2 (28.2–28.3) 2	27.6, 27.1	26.7 (26.1–27.6) 4
PB	3.3, –	9.2 (9.1–9.2) 3	6.7, 6.6	6.4 (6.0–6.9) 4
BB	7.8, –	13.0 (13.0–13.1) 3	11.9, 12.3	12.0 (11.6–12.6) 4
MB	8.8, –	14.3 (14.2–14.5) 3	14.9, 15.4	14.3 (13.7–14.6) 4
ZB	9.5, –	15.4 (15.4–15.6) 3	15.7, 16.0	15.3 (14.8–16.0) 3
MTL	5.8, –	10.4 (10.2–10.5) 2	10.0, 9.5	9.5 (9.2–9.7) 4
BAM	6.3, –	9.8 (9.7–10.0) 3	10.0, 9.9	9.8 (9.6–10.1) 4
BAC	3.5, –	6.5 (6.2–6.9) 2	7.5, 7.3	6.8 (6.6–6.9) 4

[a] AMNH 273075; MUSM 15212.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 5495, 5916, 13231.
[c] MUSM 5917, 21204.
[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of CEBIOMAS 106; MUSM 5505, 21202, 21203.

manmade structures such as culverts (Taddei, 1975; Williams and Genoways, 2008), but in caveless and roadless Amazonian landscapes this species must use other diurnal refugia. Our observation from Nuevo San Juan and Patterson's (1992) report from the Rio Juruá suggest that *M. macrophyllum* roosts in or under fallen trees, perhaps always in close proximity to water, over which this species is known to forage for insects (Meyer et al., 2005).

Phylloderma stenops Peters, 1865

Voucher material (total = 3): Jenaro Herrera (MUSM 5495, 5916), Nuevo San Juan (MUSM 13231); see table 33 for measurements.

Unvouchered observations: None.

Identification: *Phylloderma* is a monotypic genus that occurs from southern Mexico to southeastern Brazil (Williams and Genoways, 2008; Reid, 2009), but it seems to be rare (or infrequently captured) throughout its distribution (Medellín et al., 2000; Esbérard, 2012). *Phylloderma stenops* can be distinguished from other phyllostomines by the following traits: relatively large size (forearm 65–80 mm, greatest length of skull 29–32 mm); calcar equal or shorter than foot; tail extending to middle of uropatagium; face naked, with pinkish skin; horseshoe of noseleaf fused to upper lip below nostrils; wingtips whitish; rostrum shorter than braincase; two upper incisors; first lower incisor bifid; and three lower premolars, of which the second is minute (Goodwin, 1940; Barquez and Ojeda, 1979; Williams and Genoways, 2008; Reid, 2009; López-Baucells et al., 2018). Descriptions and measurements of *P. stenops* were provided by

Goodwin (1940), Husson (1962, 1978), Barquez and Ojeda (1979), Swanepoel and Genoways (1979), Lim et al. (2005), Brito M. and Arguero (2012), and Salas et al. (2014). Three subspecies are currently recognized: *P. s. septentrionalis* (southern Mexico to Costa Rica), *P. s. stenops* (Panama to southern Brazil), and *P. s. boliviensis* (central Bolivia) (Williams and Genoways, 2008).

Ascorra et al. (1993) and Fleck et al. (2002) correctly identified their specimens from Jenaro Herrera and Nuevo San Juan, respectively, as *Phylloderma stenops*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *P. stenops stenops*, with measurements that fall within the range of size variation previously documented for this taxon.

Remarks: The single nocturnal capture of *Phylloderma stenops* accompanied by ecological data from our region was in a ground-level mist-net in primary forest. No roosting groups of this species were encountered during our study.

Genus *Phyllostomus* Lacépède, 1799

The genus *Phyllostomus* includes three widespread species and one (*P. latifolius*) with a more limited distribution (Simmons, 2005; Williams and Genoways, 2008; Simmons and Cirranello, 2020). References useful for identifying species of *Phyllostomus* include Santos et al. (2003) and Williams and Genoways (2008), both of which provided keys based on external and craniodental morphology; two other references, Rodríguez-Posada and Sánchez-Palomino (2009) and López-Baucells et al. (2018) provided keys based on external characters only. We recorded all three of the widespread species in the Yavarí-Ucayali interfluve: *P. discolor*, *P. elongatus*, and *P. hastatus*.

Phyllostomus discolor (Wagner, 1843)

Voucher material (total = 6): Isla Muyuy (MUSM 21202–21204), Jenaro Herrera (CEBIOMAS 106; MUSM 5505, 5917); see table 33 for measurements.

Unvouchered observations: During the Yavarí Rapid Biological Inventory, one individual of *Phyllostomus discolor* was captured at Quebrada Buenavista, and two others were captured at Quebrada Limera (Escobedo, 2003).

Identification: *Phyllostomus discolor* is widely distributed from southern Mexico to northern Paraguay and southern Brazil (Kwiecinski, 2006; Williams and Genoways, 2008; Reid, 2009). This species is easily distinguished from other congeners by having a forearm <70 mm, a calcar shorter than the foot, and small ears (<25 mm, from notch); the sagittal crest is absent or weakly developed, and the first upper and lower incisors are broad (wider than tall) (Kwiecinski, 2006; Williams and Genoways, 2008; López-Baucells et al., 2018). Descriptions and measurements of *P. discolor* were provided by Felten (1956), Goodwin and Greenhall (1961), Husson (1962, 1978), Power and Tamsitt (1973), Taddei (1975), Swanepoel and Genoways (1979), Willig (1983), Brosset and Charles-Dominique (1990), Lim et al. (2005), Kwiecinski (2006), and Rodríguez-Posada and Sánchez-Palomino (2009).

There is currently some disagreement concerning subspecies in *Phyllostomus discolor*. Koopman (1994) recognized two: *P. d. discolor* (South America east of the Andes to northern Paraguay and southern Brazil) and *P. d. verrucosus* (southern Mexico to northwestern Peru). However, Power and Tamsitt (1973), Simmons and Voss (1998), and Rodríguez-Posada and Sánchez-Palomino (2009) did not recognize subspecies. Both Power and Tamsitt (1973) and Rodríguez-Posada and Sánchez-Palomino (2009) noted that there is no clear morphological distinction between populations on opposite sides of the Andes, and we follow those authors in choosing not to recognize subspecies in *P. discolor*.

Ascorra et al. (1993) correctly identified their material from Jenaro Herrera as *Phyllostomus discolor*. All the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *P. discolor*, and measurements fall within the range of size variation previously documented for the species.

Remarks: The only capture of *Phyllostomus discolor* accompanied by ecological information from our region was in a ground-level mistnet in primary forest at Jenaro Herrera. No roosting groups of this species were encountered during our study.

Phyllostomus elongatus
(É. Geoffroy St.-Hilaire, 1810)

Figure 19A

Voucher material (total = 24): Estación Biológica Madre Selva (MUSM 32148), Jenaro Herrera (MUSM 5494, 5530), Nuevo San Juan (AMNH 272679, 272680, 272762, 272763, 272804, 273103, 273120, 273195; MUSM 13232–13236, 15253–15255), Quebrada Blanco (MUSM 21205), Quebrada Esperanza (FMNH 89041, 89042, 89150), Quebrada Pantaleón (MUSA 15259); see table 34 for measurements.

Unvouchered observations: During the Yavarí Rapid Biological Inventory, one individual of *Phyllostomus elongatus* was captured at Quebrada Buenavista, and two individuals were captured at Quebrada Curacinha (Escobedo, 2003). An unspecified number of individuals of *P. elongatus* were also captured at Anguila and Wiswincho during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015).

Identification: *Phyllostomus elongatus* is easily distinguished from other congeners by the following combination of characteristics: medium size (forearm 61–75 mm, greatest length of skull 29–35 mm); bicolored dorsal fur; ventral fur dark with no frosting; plagiopatagium attached to the ankle; wings with white tips; calcar equal to or longer than foot; ear length (from notch) >25 mm; tibia >24 mm; and sagittal crest well developed (Williams and Genoways, 2008; Rodríguez-Posada and Sánchez-Palomino, 2009; López-Baucells et al., 2018). Descriptions and measurements of *P. elongatus* were provided by Husson (1962, 1978), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Lim et al. (2005), Rodríguez-Posada and Sánchez-Palomino (2009), and Novaes et al. (2014). No subspecies are currently recognized (Williams and Genoways, 2008; Rodríguez-Posada and Sánchez-Palomino, 2009).

Ascorra et al. (1993), Ceballos-Bendezú (1968), Fleck et al. (2002), and Medina et al. (2015) correctly identified their specimens from Jenaro Herrera, Quebrada Esperanza, Nuevo San Juan, and Quebrada Pantaleón, respectively, as *Phyllostomus elongatus*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *P. elongatus*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: All the nocturnal captures of *Phyllostomus elongatus* accompanied by ecological data from our region (N = 29) were in ground-level mistnets. Of these, 20 were in primary forest, 3 were in secondary vegetation, and 6 were in a palm swamp (*aguajal*). We found five roosts of this species near Nuevo San Juan (table 35), usually in the rotted-out central cavities of large standing trees, but once beneath an undercut stream bank; recorded heights of roosting groups ranged from ground level to 4 m above the ground. Four roosts were in primary upland forest, and one was in seasonally flooded forest. Two roosts contained only *P. elongatus*, one was shared with *P. hastatus*, another with *Carollia perspicillata*, and one was shared with an unidentified species that evaded capture.

Our observation of *Phyllostomus elongatus* roosting beneath an undercut stream bank is unique; all other reported natural roosts of this widespread species suggest that, in caveless landscapes, this species roosts almost exclusively in hollow trees (Tuttle, 1970; Ibáñez, 1981; Simmons and Voss, 1998; Aguirre et al., 2003; Shapley et al., 2005; Díaz and Linares García, 2012).

Phyllostomus hastatus (Pallas, 1767)

Figure 19B

Voucher material (total = 27): Jenaro Herrera (AMNH 278513; MUSM 840, 875, 876, 5507), Nuevo San Juan (AMNH 272681, 272682,

FIG. 19. Photographs of **A,** an adult *Phyllostomus elongatus* captured at Quebrada Blanco; and **B,** an adult female (ROM 122132) *P. hastatus* captured at Jenaro Herrera. Photographs by Marco Tschapka (A) and Burton Lim (B).

TABLE 34

External and Craniodental Measurements (mm) and Weights (g) of *Phyllostomus elongatus* and *P. hastatus* from the Yavarí-Ucayali Interfluve

	P. elongatus		*P. hastatus*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	38.4 (32.0–44.0) 10	36.7 (32.9–42.0) 10	95.2 (72.0–110.0) 12	86.2 (79–94) 6
ToL	102.7 (95–114) 11	104.7 (94–113) 11	133.6 (120–145) 12	131.0 (124–139) 6
LT	18.8 (15–24) 11	20.8 (16–24) 11	21.4 (18–25) 12	20.7 (17–23) 6
HF	17.1 (16–18) 11	16.4 (15–18) 12	20.8 (17–24) 12	20.3 (17–22) 7
E	29.2 (28–30) 11	29.3 (27–31) 11	31.6 (28–33) 12	31.5 (30–33) 6
F	65.6 (63.0–69.0) 11	65.4 (64.0–68.0) 12	86.0 (81.0–90.0) 12	84.6 (83.0–86.0) 7
GLS	28.4 (27.5–29.5) 4	28.7 (28.2–29.3) 7	36.8 (35.0–38.3) 6	36.6 (36.1–37.7) 4
CIL	25.8 (25.4–26.5) 4	25.9 (25.5–26.3) 7	33.5 (32.8–34.4) 6	33.1 (32.6–33.6) 4
PB	5.5 (5.4–5.5) 4	5.3 (5.2–5.5) 7	7.1 (6.8–7.4) 6	7.3 (6.8–7.5) 4
BB	10.9 (10.7–11.1) 4	10.9 (10.5–11.2) 7	14.4 (13.8–14.4) 6	13.9 (13.2–14.4) 4
MB	14.1 (13.4–14.8) 4	14.0 (13.6–14.2) 6	19.1 (18.1–20.1) 6	18.9 (18.3–19.4) 4
ZB	16.1 (15.8–16.7) 4	16.0 (15.8–16.3) 6	20.3 (19.3–21.1) 6	20.1 (19.5–20.5) 4
MTL	10.7 (10.5–11.0) 4	10.6 (10.4–10.7) 7	13.3 (13.2–13.4) 6	13.2 (12.8–13.4) 4
BAM	10.9 (10.8–11.1) 4	11.2 (10.9–11.6) 7	13.5 (13.2–13.9) 6	13.8 (13.4–14.1) 4
BAC	7.6 (7.4–7.8) 4	7.4 (7.3–7.7) 7	9.3 (8.7–9.7) 6	9.3 (9.1–9.6) 4

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272679, 272762, 272804, 273103, 273120; FMNH 89041; MUSM 13233, 13234, 15254, 15255, 32148.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272680, 272763, 273195; FMNH 89042, 89150; MUSM 5494, 5530, 13232, 13235, 13236, 15253, 21205.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272682, 272754, 273073, 273090, 273154, 278513; MUSM 875, 5507, 13237, 13239, 15257, 15258.
[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74099, 272681, 272755; MUSM 840, 876, 13238, 13240, 15256.

272754, 272755, 273073, 273090, 273154; MUSM 13237–13240, 15256–15258), Orosa (AMNH 74098, 74099), Quebrada Betilia (MUSA 15198), Quebrada Lobo (MUSA 15141), Quebrada Sábalo (MUSA 15210, 15229, 15230), Río Blanco (MUSA 15094); see table 34 for measurements.

Unvouchered observations: An unspecified number of individuals of *Phyllostomus hastatus* were observed at Quebrada Pobreza during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015). This species was also identified using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Phyllostomus hastatus* is easily distinguished from other congeners by the following combination of characteristics: large size (forearm >75 mm, greatest length of skull >35 mm); plagiopatagium attached to side of foot; calcar equal to or longer than foot; ear length (from notch) >25 mm; and sagittal crest well developed (Williams and Genoways, 2008; López-Baucells et al., 2018). Descriptions and measurements of *P. hastatus* were provided by Goodwin and Greenhall (1961), Husson (1962, 1978), Taddei (1975), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Santos et al. (2003), Lim et al. (2005), and Rodríguez-Posada and Sánchez-Palomino (2009).

There is some disagreement concerning the recognition of subspecies in *Phyllostomus hasta-*

TABLE 35

Roosting Groups of *Phyllostomus elongatus* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
20 Sep 1999	cavity in standing tree	1	yes	1 ad. male
28 Sep 1999	undercut earth bank	1	yes	1 ad. female
28 Sep 1999	cavity in standing tree	2	no	1 ad. male
15 Oct 1999	cavity in standing tree	unknown	unknown	1 ad. male
8 Nov 1999	cavity in standing tree	8	no	1 ad. male, 2 ad. females, 2 juv.

tus. Koopman (1994) and Santos et al. (2003) recognized two: *P. h. panamensis* (Honduras to Peru and Venezuela) and *P. h. hastatus* (eastern Venezuela to northern Bolivia and southeastern Brazil). By contrast, Williams and Genoways (2008) recognized three: *P. h. aruma* (Tocantins, Brazil); *P. h. hastatus* (eastern Venezuela to northern Bolivia and southeastern Brazil); and *P. h. panamensis* (Honduras to western and northern Colombia and northern Venezuela). Rodríguez-Posada and Sánchez-Palomino (2009) hypothesized that *P. h. hastatus* occurs east of the Andes whereas populations of *P. h. panamensis* occur west of the Andes. Under any of these trinomial classifications, our material would be expected to belong to the nominotypical subspecies.

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified specimens from Jenaro Herrera, Nuevo San Juan, Quebrada Betilia, Quebrada Lobo, Quebrada Sábalo, and Río Blanco as *Phyllostomus hastatus*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *P. hastatus hastatus*, with measurements that fall within the range of size variation previously documented for that taxon.

Remarks: Of 73 nocturnal captures of *Phyllostomus hastatus* accompanied by ecological data from our region, 65 were in ground-level nets and 8 were in elevated nets. Forty-eight mistnet captures were in primary forest, 8 were in secondary vegetation, 16 were in clearings, and 1 was in a swampy mineral lick (*collpa*). In May and June of 1998 we mistnetted many individuals of *Phyllostomus hastatus* that were covered in the yellow-green pollen of balsa trees (Malvaceae: *Ochroma pyramidale*), which were then mass-flowering along the banks of the nearby Río Gálvez.

We found four roosting groups of *Phyllostomus hastatus* near Nuevo San Juan. The first, encountered on 9 September 1999, consisted of a single adult male that was roosting with *Lophostoma silvicolum* in a hollowed-out arboreal termite nest about 4 m above the ground in young secondary vegetation. The second, encountered on 15 September 1999, consisted of three individuals (of which one adult male and one adult female were collected) that occupied an abandoned woodpecker hole about 9 m above the ground in an *Astrocaryum jauari* palm on the bank of the Río Gálvez. The third, encountered on 23 September 1999, consisted of seven individuals (of which one adult male and five adult females were collected) that occupied an abandoned woodpecker hole about 9 m above the ground in the swollen part of the trunk of an *Iriartea deltoidea* palm in primary hilltop forest. The fourth, encountered on 22 October 1999, consisted of a single adult male roosting in the company of *Carollia perspicillata* and *Molossus rufus* in another cavity that may have originally been excavated by woodpeckers, about 25 m above the ground in the trunk of a large dicotyledonous tree in primary floodplain forest near an oxbow lake.

Hollow trees and termite nests seem to be the most commonly encountered types of roosts for *Phyllostomus hastatus* throughout its extensive

TABLE 36

External and Craniodental Measurements (mm) and Weights (g) of *Tonatia maresi* and *Trachops cirrhosus* from the Yavarí-Ucayali Interfluve

	Tonatia maresi		*Trachops cirrhosus*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	25.0, 30.0	26.5 (22.0–29.0) 5	30.2 (21–39.4) 9	41.6 (31–54) 4
ToL	92, 85	97.8 (88–107) 6	96.7 (85–106) 11	99.0 (93–103) 7
LT	20, 17	20.7 (17–24) 6	17.1 (11–23) 11	17.1 (15–19) 7
HF	15, 15	15.5 (13–17) 6	18.3 (16–20) 11	18.9 (17–20) 7
E	28, 28	30.3 (28–32) 6	33.3 (30–35) 11	33.6 (33–34) 7
F	55.0, 58.0	57.4 (56.0–59.0) 6	58.9 (55.0–62.0) 11	63.3 (61.0–66.0) 7
GLS	26.4, 27.7	27.2 (26.7–27.7) 2	27.8 (26.0–28.7) 9	28.4 (27.8–29.1) 7
CIL	23.6, 24.5	24.5 (24.1–24.8) 2	25.5 (23.6–26.8) 9	26.0 (25.4–26.7) 7
PB	5.4, 5.5	5.4 (5.2– 5.5) 2	5.4 (5.0–5.6) 9	5.2 (5.1–5.5) 7
BB	10.0, 10.3	10.6 (10.5–10.8) 2	11.6 (11.2–12.2) 9	11.5 (11.0–11.7) 7
MB	12.1, 12.5	12.8 (12.7–13.0) 2	13.5 (12.8–14.1) 9	13.5 (13.0–14.0) 7
ZB	13.1, 14.5	14.0 (13.5–14.5) 2	14.6 (13.6–15.1) 8	14.4 (14.0–14.7) 7
MTL	9.5, 9.7	9.6 (9.5–9.7) 2	10.4 (9.8–10.7) 9	10.7 (10.5–11.0) 7
BAM	8.2, 9.0	8.8 (8.7–8.9) 2	10.1 (9.8–10.3) 9	10.2 (9.8–10.7) 7
BAC	5.4, 5.6	5.6 (5.5–5.7) 2	6.1 (5.4–6.4) 9	6.2 (6.0–6.6) 7

[a] AMNH 278467, 278484.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272812; CEBIOMAS 110, 111; MUSM 5549, 13270, 13271.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272820, 273176, 278476; CEBIOMAS 112; FMNH 89031, 89032; MUSM 5533, 13277–13280.

[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272813, 272821; FMNH 89033–89035; MUSM 15286, 15287.

geographic range, although it has also been found roosting in caves and foliage (see literature reviewed by Voss et al., 2016).

Tonatia maresi Williams et al., 1995

Figure 20A

Voucher material (total = 8): Jenaro Herrera (AMNH 278467, 278484; CEBIOMAS 110, 111; MUSM 5549), Nuevo San Juan (AMNH 272812; MUSM 13270, 13271); see table 36 for measurements.

Unvouchered observations: One individual of *Tonatia maresi* (identified as *T. saurophila*) was captured and released at Divisor during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006). Another individual was captured at Frog Valley on 17 February 2019.

Identification: The genus *Tonatia* has a complex taxonomic history. Up until 2002, this genus was thought to include six or seven species, but Lee et al. (2002) demonstrated that these did not comprise a monophyletic group and transferred most of them to the genus *Lophostoma,* restricting *Tonatia* to just the type species (*T. bidens*) and its close relative, *T. saurophila*. Previously, the name *bidens* had been applied to all living members of the latter group, but Williams et al. (1995) had shown that it includes two species, with *T. bidens* restricted to the Atlantic Forest (southeastern Brazil, north-

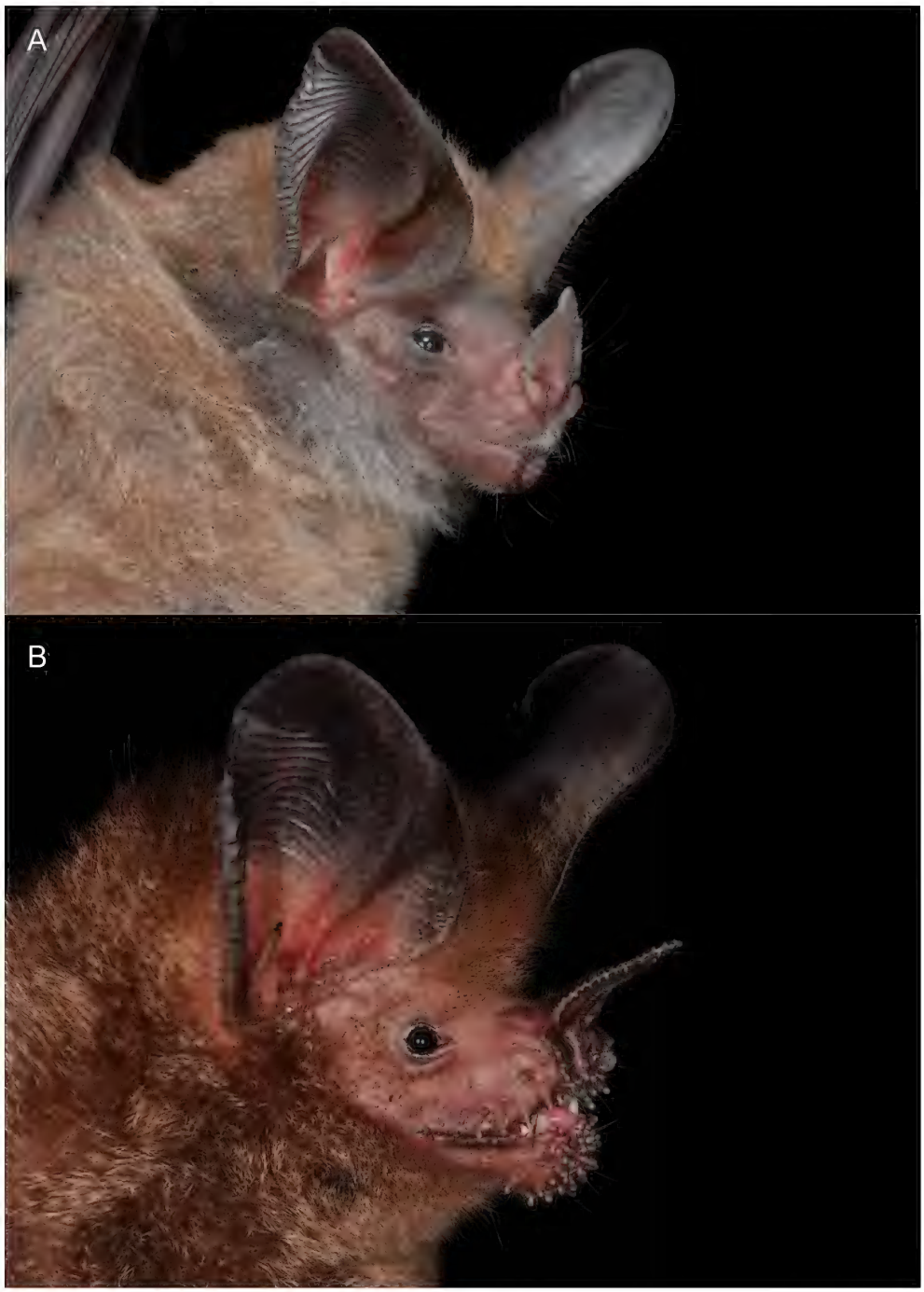


FIG. 20. Photographs of **A,** an adult male (ROM 122096) *Tonatia maresi* and **B,** an adult *Trachops cirrhosus*, both captured at Jenaro Herrera. Photographs by Burton Lim (A) and Marco Tschapka (B).

eastern Argentina, and eastern Paraguay), whereas the name *T. saurophila* (originally based on Jamaican fossil material) applied to populations in Mexico, Central America, the Caribbean, and northern South America. *Tonatia saurophila* thus conceived included three subspecies: *T. s. bakeri*, *T. s. maresi*, and *T. s. saurophila* (see Williams et al., 1995; Williams and Genoways, 2008). Most recently, Basantes et al. (2020) conducted thorough morphological, morphometric, and molecular analyses of this group and concluded that *T. saurophila* as defined by Williams et al. (1995) is a complex that includes three valid species: *Tonatia saurophila* appears to be an extinct island form, whereas living populations formerly referred to that species represent either *T. maresi* (east of the Andes) or *T. bakeri* (from southeastern Mexico southward into northern Colombia, northwestern Venezuela, and northwestern Ecuador).

Tonatia maresi can be distinguished from other species in the genus by the following combination of traits: small size (forearm 53–60 mm, condylocanine length 22–25 mm); skin around the mouth, noseleaf, and warts of the lower lip darkly pigmented; posterior edge of the cranium with a blunt vertex due to a weakly developed sagittal crest; slender mandibular condyles; canine and first lower premolar separated by a diastema; and clinoid process poorly developed or absent. In the field, living individuals of *Tonatia maresi* can be distinguished from *Lophostoma silvicolum* (which they resemble in size and external morphology) by the "ear test": touching the ears in *Lophostoma* will cause the bat to fold them down over the top of the head, a behavior that is not observed in *Tonatia*. Descriptions and measurements of *T. maresi* (usually identified as *T. bidens* or *T. saurophila*) have been provided by Goodwin and Greenhall (1961), Genoways and Williams (1980), Genoways and Williams (1984), Brosset and Charles-Dominique (1990), Williams et al. (1995), Simmons and Voss (1998), and Lim et al. (2005). No subspecies are currently recognized (Basantes et al., 2020).

Ascorra et al. (1993) erroneously identified one specimen (MUSM 5549) from Jenaro Herrera as *Tonatia silvicola* (= *Lophostoma silvicolum*), but Fleck et al. (2002) correctly identified their specimens from Nuevo San Juan as *T. saurophila*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *T. maresi*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: All nocturnal captures of *Tonatia maresi* accompanied by ecological data from our region (N = 10) were in ground-level mistnets. Of these, 7 were in primary forest, 1 was in secondary vegetation, 1 was in a swampy mineral lick (*collpa*), and 1 was in a palm swamp (*aguajal*). No roosting groups of *Tonatia maresi* were encountered during our study.

Trachops cirrhosus (Spix, 1823)

Figure 20B, 21

Voucher material (total = 19): Jenaro Herrera (AMNH 278476; CEBIOMAS 112; MUSM 5533), Nuevo San Juan (AMNH 272813, 272820, 272821, 273176; MUSM 13277–13280, 15286, 15287), Orosa (AMNH 74026), Quebrada Esperanza (FMNH 89031–89035); see table 36 for measurements.

Unvouchered observations: During the Yavarí Rapid Biological Inventory, *Trachops cirrhosus* was captured at Quebrada Buenavista (one individual) and Quebrada Curacinha (two individuals; Escobedo, 2003). An unspecified number of individuals of *Trachops cirrhosus* were also captured at Anguila and Wiswincho during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015). Five individuals were captured at Frog Valley on 17 February 2019, and another 23 individuals were captured at the same locality on 20 February 2019.

Identification: *Trachops* is a widespread monotypic genus distributed from southern Mexico to southeastern Brazil (Cramer et al., 2001; Williams and Genoways, 2008; Reid, 2009).

FIG. 21. *Trachops cirrhosus* flying at Frog Valley. Photograph by Brock Fenton.

Trachops cirrhosus is easily distinguished from other phyllostomines by having many fleshy elongated warts on the chin and lips, finely serrated noseleaf margins, a tail that extends to the middle of the uropatagium, a calcar with the same length as the foot, and two pairs of lower incisors (Williams and Genoways, 2008; Reid, 2009; López-Baucells et al., 2018). Descriptions and measurements of *T. cirrhosus* were provided by Ruschi (1953), Burt and Stirton (1961), Goodwin and Greenhall (1961), Husson (1962, 1978), Starrett and Casebeer (1968), Swanepoel and Genoways (1979), Willig (1983), Brosset and Charles-Dominique (1990), Alvarez-Castañeda and Alvarez (1991), Simmons and Voss (1998), Cramer et al. (2001), Lim et al. (2005), and Feijó and Nunes (2010). Three subspecies are currently recognized: *T. c. cirrhosus* (Costa Rica southeastward to northern Bolivia and central Brazil), *T. c. coffini* (southern Mexico to Nicaragua), and *T. c. ehrhardti* (southern Brazil) (Cramer et al., 2001; Williams and Genoways, 2008). It is possible that some or all of these taxa represent distinct species (Ditchfield, 2000; Clare, 2011) but we recommend continued treatment of them as conspecific pending completion of a thorough revision of the genus. Regardless, if subspecies are recognized, material from our study area represents the nominotypical subspecies.

Ascorra et al. (1993) and Fleck et al. (2002) correctly identified their specimens from Jenaro Herrera and Nuevo San Juan, respectively, as *Trachops cirrhosus*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous qualitative and morphometric descriptions of the species.

Remarks: All 15 recorded nocturnal captures of *Trachops cirrhosus* from our region were made in ground-level mistnets: of these, 8 were in primary forest, 1 was in secondary vegetation, 2 were in a swampy mineral lick (*collpa*), and 4 were in a palm swamp (*aguajal*). We found three roosting groups of *Trachops cirrhosus* near Nuevo San Juan. The first group, encountered on 25

October 1999, consisted of a single adult male roosting in the company of *Lampronycteris brachyotis* and *Carollia perspicillata* about 18 m above the ground in the hollowed-out central cavity of a large standing tree in primary floodplain forest. The second roosting group, encountered on 1 November 1999, consisted of about 11 individuals (of which three adult females were captured) inside a hollow log in primary valley-bottom upland forest. The third group, also encountered on 1 November 1999, consisted of about nine individuals (of which four adult females were captured), likewise inside a hollow log, but in primary hillside forest. At Frog Valley we captured 23 individuals of *T. cirrhosus* as they emerged from this roost along with *Peropteryx pallidoptera, P. macrotis*, *Hsunycteris pattoni*, and *Carollia brevicauda*, but many emerging bats escaped, so no exact counts are available (see the account for *P. macrotis*, above).

Cavities in standing trees seems to be the predominant type of natural roost in which *Trachops cirrhosus* is normally found in both Central and South America (Voss et al., 2016), although hollow logs are clearly also used, as we discovered near Nuevo San Juan and at Frog Valley.

Vampyrum spectrum (Linnaeus, 1758)

Voucher material: None.

Unvouchered observations: Ascorra et al. (1991) reported capturing an unspecified number of individuals of *Vampyrum spectrum* at Jenaro Herrera (see Remarks, below).

Identification: *Vampyrum*, the largest bat in the Neotropics, is a monotypic genus that occurs from southern Mexico to Bolivia and southwestern Brazil (Williams and Genoways, 2008; Reid, 2009). *Vampyrum spectrum* can be easily distinguished from other phyllostomines by the following traits: very large size (forearm 98–118 mm, greatest length of skull 49–54 mm); large ears; tail absent; calcar longer than foot; rostrum as long as braincase; three lower premolars; and two pairs of lower incisors (Williams and Genoways, 2008; Reid, 2009; Díaz, 2011; López-Baucells et al., 2018). Descriptions and measurements of *V. spectrum* were provided by Goodwin and Greenhall (1961), Husson (1962, 1978), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Navarro and Wilson (1982), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Vargas-Espinoza et al. (2004), Discher et al. (2009), Díaz (2011), and Sousa et al. (2011). No subspecies are currently recognized (Williams and Genoways, 2008).

Vampyrum spectrum is morphologically unmistakable, so we see no reason to doubt Ascorra et al.'s (1993) identification of the individuals they captured and released at Jenaro Herrera. Their single reported forearm measurement (117 mm, from a female) is consistent with the known range of morphometric variation in this species and is much too large for the forearm of any other Neotropical bat.

Remarks: Ascorra et al. (1993) reported that at least one of the individuals they captured was caught in a mistnet, where it was feeding on a *Carollia benkeithi* (identified as *C. castanea*).

Subfamily Rhinophyllinae Baker et al., 2016

Rhinophyllinae comprises one genus and three species that were traditionally classified in the subfamily Carolliinae (Simmons and Voss, 1998; Wetterer et al., 2000; Simmons, 2005; McLellan and Koopman, 2008). However, phylogenetic analyses of molecular data have shown that *Rhinophylla* is not the sister taxon of *Carollia* but, instead, is more closely related to the subfamily Stenodermatinae (Baker et al., 2003; Dávalos et al., 2012; Dávalos et al., 2014; Rojas et al., 2016). Although Rhinophyllinae was first proposed by Baker et al. (2003), the name was not made available until the joint publications of Baker et al. (2016) and Cirranello et al. (2016). Bats in this subfamily are characterized by the following characteristics: dorsal fur unicolored; vibrissal papillae surrounding noseleaf joined to form a skin flap; uropatagium relatively short; external tail absent; central tubercle on lower lip flanked by a single large, lobate, padlike tubercle on each side; first and second phalanges of digit IV

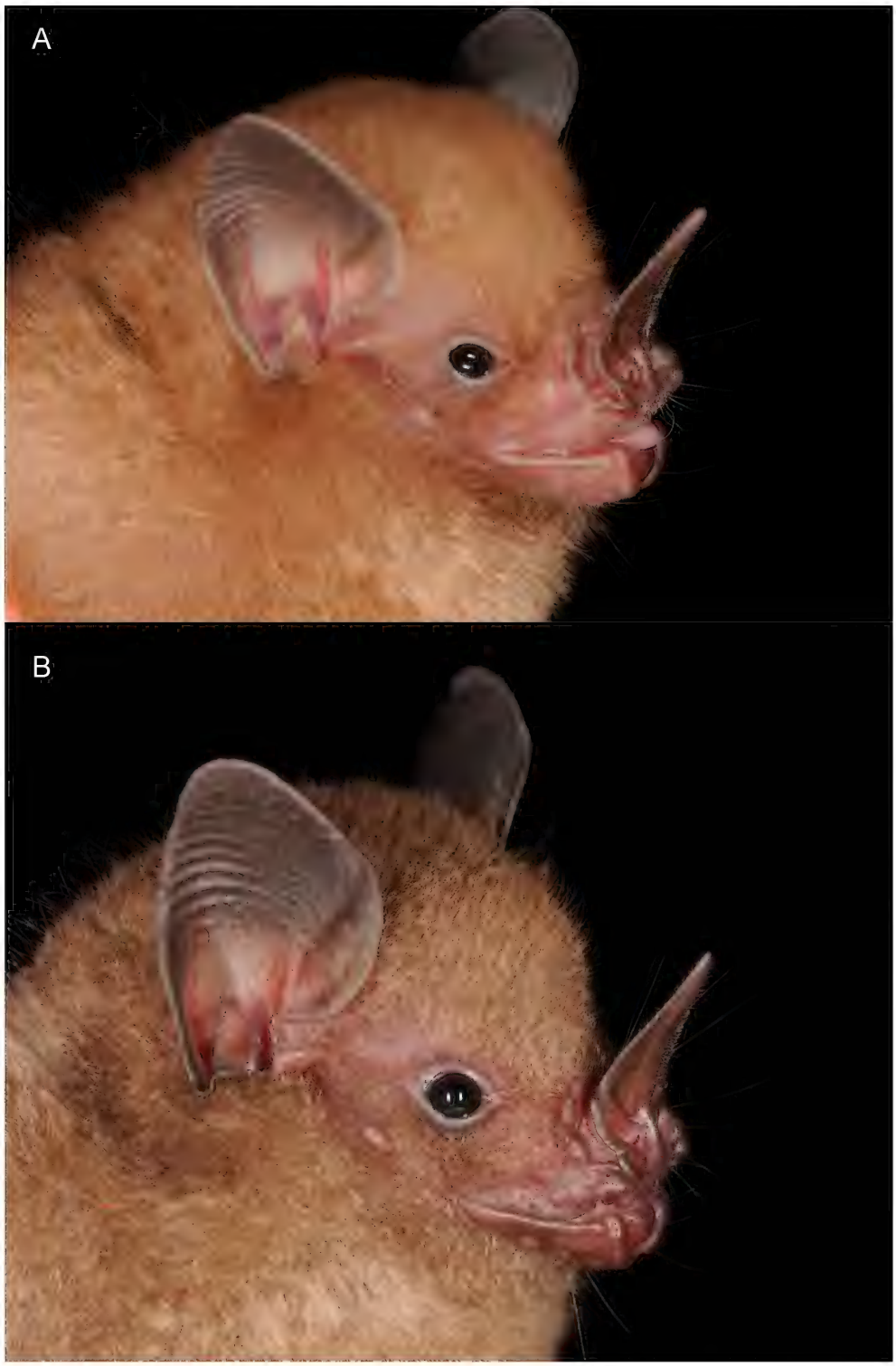


FIG. 22. Photographs of **A,** an adult *Rhinophylla fischerae* and **B,** an adult *R. pumilio*, both captured at Jenaro Herrera. Photographs by Marco Tschapka.

TABLE 37

External and Craniodental Measurements (mm) and Weights (g) of *Rhinophylla fischerae* and *R. pumilio* from the Yavarí-Ucayali Interfluve

	R. fischerae		*R. pumilio*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	7.4 (6.3–8.5) 4	7.5 (5.9–10.0) 5	8.7 (7.2–12.0) 11	10.6 (7.8–21.0) 13
ToL	47.0 (45–49) 4	47.8 (46–50) 6	49.9 (43–55) 11	51.2 (45–55) 13
HF	9.0 (8–10) 4	8.3 (7–10) 6	8.9 (8–10) 13	9.2 (7–10) 15
E	14 (13–15) 4	14.2 (13–15) 6	14.7 (13–16) 11	15.7 (12–18) 13
F	31.0 (30.0–32.0) 4	31.3 (31.0–32.0) 6	33.7 (32.4–35.0) 13	34.8 (33.0–36.0) 15
GLS	16.2 (15.6–16.7) 2	16.4 (16.1–16.6) 3	17.9 (17.4–18.4) 6	18.2 (17.6–19.0) 6
CIL	14.5 (14.0–15.1) 2	15.1 (15.0–15.1) 3	16.3 (15.8–16.5) 6	16.9 (16.3–17.7) 7
PB	5.0 (4.9–5.1) 2	5.0 (4.9–5.0) 3	5.4 (5.2–5.7) 6	5.3 (5.1–5.6) 7
BB	7.7 (7.5–7.8) 2	7.8 (7.7–7.9) 3	8.2 (7.9–8.4) 6	8.1 (7.8–8.5) 7
MB	8.3	8.5 (8.4–8.7) 3	9.0 (8.8–9.4) 6	9.1 (8.8–9.6) 7
MTL	4.5 (4.3–4.7) 2	4.4 (4.3–4.4) 3	4.9 (4.7–5.1) 6	5.1 (4.9–5.3) 7
BAM	5.9 (5.8–6.1) 2	6.1 (5.8–6.4) 3	6.4 (6.1–6.7) 6	6.5 (6.3–6.7) 7
BAC	4.4 (4.2–4.7) 2	4.5 (4.4–4.5) 3	4.5 (4.4–4.7) 6	4.7 (4.5–4.9) 7

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272830; CEBIOMAS 107; MUSM 13243, 31585.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272803, 272822, 278505; MUSM 5550, 13244, 31584.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272767, 272845, 272868, 273041, 278487; MUSM 843, 844, 858, 13245, 13247, 21245, 21246, 31517.

[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273137, 273158, 273159; CEBIOMAS 108; LSUMZ 28434, 28435; MUSM 841, 842, 859, 13246, 15260, 15261, 15263, 21243, 31617.

subequal in length; upper molars lacking a protocone; and lower molars lacking a metaconid and resembling lower premolars (McLellan and Koopman, 2008; Cirranello et al., 2016; López-Baucells et al., 2018). Rinehart and Kunz (2006) and McLellan and Koopman (2008) provided a key to the species of *Rhinophylla* based on external and craniodental characters. We recorded both species that are expected to occur in the Yavarí-Ucayali interfluve.

Rhinophylla fischerae Carter, 1966

Figure 22A

Voucher material (total = 14): Estación Biológica Madre Selva (MUSM 31584, 31585), Jenaro Herrera (AMNH 278505; CEBIOMAS 107; MUSM 5550), Nuevo San Juan (AMNH 272803, 272822, 272830; MUSM 13243, 13244), Quebrada Betilia (MUSA 15162, 15163), Quebrada Lobo (MUSA 15131), Quebrada Sábalo (MUSA 15234); see table 37 for measurements.

Unvouchered observations: An unspecified number of individuals of *Rhinophylla fischerae* were captured at Anguila during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015). Additionally, we captured two individuals at Frog Valley on 17 February 2019.

Identification: *Rhinophylla fischerae* is easily distinguished from congeneric taxa by the following characteristics: pelage brown to reddish brown; free margin of uropatagium with a fringe of hair; forearm ≤34 mm; inner upper incisors relatively narrow, with two well-defined lobes; and a gap between the outer upper incisor and the canine (McLellan and Koop-

man, 2008; López-Baucells et al., 2018). Descriptions and measurements were provided by Carter (1966), Marinkelle and Cadena (1972), Mumford (1975), and Swanepoel and Genoways (1979).

No subspecies are currently recognized (McLellan and Koopman, 2008), but Gomes et al. (2010) suggested that *Rhinophylla fischerae* might represent a species complex based on karyotypic differences between their specimens from Brazil (with $2n = 38$, FN = 68) and Baker and Bleir's (1971) sample from Colombia (with $2n = 34$, FN = 56). Our comparisons of voucher material from the Yavarí-Ucayali interfluve with specimens from other localities across the range of the species—e.g., Brazil (AMNH 94555, 94557) and Peru (AMNH 230485, 230492)—revealed no clear morphological pattern to suggest that *R. fischerae* represents a species complex. Further studies including both mitochondrial and nuclear markers are necessary to resolve this issue.

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified the material from Jenaro Herrera, Nuevo San Juan, Quebrada Betilia, Quebrada Lobo, and Quebrada Sábalo as *Rhinophylla fischerae*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the previously documented range of size variation for *R. fischerae*.

Remarks: All the recorded captures of *Rhinophylla fischerae* accompanied by ecological information from our region ($N = 19$) were made in ground-level mistnets; of these, 11 were in primary forest, 5 were in secondary vegetation, 1 was in a swampy mineral lick (*collpa*), 1 was in a palm swamp (*aguajal*), and 1 was on a river beach. No roosting groups of this species were encountered during our study.

Rhinophylla pumilio Peters, 1865

Figure 22B

Voucher material (total = 33): Estación Biológica Madre Selva (MUSM 31517, 31617), Jenaro Herrera (AMNH 278487; CEBIOMAS 108; MUSM 841–844, 858, 859), Nuevo San Juan (AMNH 272767, 272845, 272868, 273041, 273137, 273158, 273159; MUSM 13245–13247, 15260–15263), Quebrada Blanco (MUSM 21243, 21245–21246), Quebrada Sábalo (MUSA 15233, 15235), Quebrada Vainilla (LSUMZ 28434, 28435), Río Blanco (MUSA 15081, 15086); see table 37 for measurements.

Unvouchered observations: During the Sierra del Divisor Rapid Biological Inventory, *Rhinophylla pumilio* was captured at Divisor (two individuals) and Tapiche (one individual) (Jorge and Velazco, 2006). Additionally, we captured three individuals at Frog Valley on 17 February 2019. This species was also recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Rhinophylla pumilio* is easily distinguished from other congeners by the following combinations of characteristics: margin of uropatagium naked; forearm ≥33 mm; inner upper incisors relatively broad, with three or four well-defined lobes; and no gap between the outer upper incisor and the canine (McLellan and Koopman, 2008; López-Baucells et al., 2018). Descriptions and measurements of *R. pumilio* have been provided by Husson (1962, 1978), Hill (1964), Carter (1966), Marinkelle and Cadena (1972), Swanepoel and Genoways (1979), Williams and Genoways (1980a), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Lim et al. (2005), Rinehart and Kunz (2006), and Velazco and Patterson (2019). No subspecies are currently recognized (McLellan and Koopman, 2008).

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their material from Jenaro Herrera, Nuevo San Juan, Quebrada Sábalo, and Río Blanco as *Rhinophylla pumilio*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *R. pumilio*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Of 35 recorded nocturnal captures of *Rhinophylla pumilio* accompanied by ecologi-

cal information, 32 were in ground-level nets and 3 were in elevated nets. Of these combined mistnet captures, 24 were made in primary forest, 5 in secondary vegetation, 2 in clearings, and 4 on river beaches.

We found four roosting groups of *Rhinophylla pumilio*, all of them in foliage, near Nuevo San Juan. The first roost, encountered on 10 July 1998, consisted of a single adult male in a tent made from the leaf of a hemiepiphytic aroid (?*Philodendron* sp.) about 6 m above the ground on the trunk of a *Cecropia* tree in secondary vegetation; this tent had previously been occupied by a group of four *Artibeus gnomus*, which were collected on 8 July 1998 (see below). The second group, encountered on 4 September 1999, consisted of an adult male and an adult female in a tent made from the leaf of another hemiepiphytic aroid[11] about 2 m above the ground on the trunk of a large tree in valley-bottom primary forest. The third roosting group, encountered on 11 October 1999, consisted of four individuals (of which two adult females and a juvenile female were collected) in a tent made from the bifid leaf of an understory palm (*Geonoma* sp.) in primary upland forest. The fourth group, encountered on 17 October 1999, consisted of four individuals (of which one adult male and two adult females were collected) in a tent made from the leaf of an unidentified hemiepiphyte on the trunk of a tree in primary upland forest.

Rhinophylla pumilio is the only non-stenodermatine phyllostomid known to roost in modified-foliage shelters ("tents"), but it is not known whether or not this species itself modifies leaves for this purpose. Our observation of *R. pumilio* roosting in a leaf tent previously occupied by *Artibeus gnomus* is the second known case of this species appropriating such a shelter following the removal of its stenodermatine inhabitants (Simmons and Voss [1998: 96] reported *R. pumilio* roosting in a tent previously occupied by *Mesophylla macconnelli*). Both observations are consistent with the suggestion by Charles-Dominique (1993) that *Rhinophylla pumilio* opportunistically uses shelters made by other species, although it also roosts in unmodified foliage (Henry and Kalko, 2007).

[11] Possibly the same species as the hemiepiphyte observed in 1998. According to the hunter who accompanied D.W.F., this plant is called senad chispan dawë in the Matses language.

Subfamily Stenodermatinae Gervais, 1855

One hundred species in 19 genera are currently recognized in the phyllostomid subfamily Stenodermatinae (Cirranello et al., 2016; Garbino et al., 2020; Simmons and Cirranello, 2020). Members of this subfamily are characterized by calcar absent or shorter than foot; lack of an externally visible tail; noseleaf (when present) with spear equal to or longer than twice the height of the horseshoe; papillae present on inner surface of lips and cheeks; lateral circumvallate papillae present on dorsolateral border of tongue; infraorbital foramen located above posterior half of second upper premolar; zygomatic arch complete; and molars low crowned but always with well-developed cusps (Gardner, 2008d; Cirranello et al., 2016). We recorded all 28 stenodermatine species that are expected to occur in the Yavarí-Ucayali interfluve.

Genus *Artibeus* Leach, 1821

The genus *Artibeus* currently includes 24 species grouped into two subgenera, *Artibeus* and *Dermanura* (Hoofer et al., 2008; Redondo et al., 2008; Solari et al., 2009; Cirranello et al., 2016; Simmons and Cirranello, 2020). For decades there has been controversy as to whether three genera (*Artibeus*, *Dermanura*, and *Koopmania*), two genera (*Artibeus* and *Dermanura*), or only one genus (*Artibeus*) should be recognized in classifications of these taxa. Cirranello et al. (2016) and Baker et al. (2016) recently argued for recognition of a single genus with two subgenera, and we follow their recommendations here. Species of *Artibeus* can be distinguished from other stenodermatines by a combination of the following characteristics: pale middorsal stripe absent; skull relatively short

and broad; dental formula I 2/2, C 1/1, P 2/2, M 2–3/2–3; occlusal margins of inner upper incisors each with two subequal lobes; canines well developed and unicuspid; upper premolars each with a large, triangular labial cusp and a low, broad, and somewhat concave lingual basin; and tongue with a band of long-tipped, bifid, anterior mechanical papillae at juncture between anterior and medial-posterior mechanical papillae (Marques-Aguiar, 2008a; Cirranello et al., 2016). We recorded all nine species of *Artibeus* that are expected to occur in the Yavarí-Ucayali interfluve.

Artibeus (*Artibeus*) *concolor* Peters, 1865

Voucher material (total = 6): Jenaro Herrera (MUSM 1321, 5513, 5514, 6967, 6968; 6970); see table 38 for measurements.

Unvouchered observations: None.

Identification: *Artibeus concolor* is a widespread Amazonian species (Ascorra et al., 1993; Marques-Aguiar, 2008a). It can be distinguished from other congeners by the following combination of characteristics: medium size (forearm 43–52 mm, greatest length of skull 20.6–22.5 mm), gray-brown to brownish tricolored dorsal fur, shoulders and venter paler than dorsum, lack of facial stripes, plagiopatagium attached to leg at the base of the toes, paraoccipital processes weakly developed or absent, M1 with weakly developed hypocone, and upper and lower third molars present (Acosta and Owen, 1993; Simmons and Voss, 1998; Marques-Aguiar, 2008a; López-Baucells et al., 2018). Descriptions and measurements of *A. concolor* were provided by Husson (1962, 1978), Gardner (1976), Carter and Dolan (1978), Genoways and Williams (1979), Swanepoel and Genoways (1979), Handley (1987), Brosset and Charles-Dominique (1990), Acosta and Owen (1993), Simmons and Voss (1998), and Lim et al. (2005). No subspecies are currently recognized (Marques-Aguiar, 2008a).

Ascorra et al. (1993) correctly identified their specimens from Jenaro Herrera, which conform to previous qualitative and morphometric descriptions of *Artibeus concolor*.

Remarks: No ecological information is available for *Artibeus concolor* in our region.

Artibeus (*Artibeus*) *lituratus* (Olfers, 1818)

Figure 23A

Voucher material (total = 14): Estación Biológica Madre Selva (MUSM 32445, 32446), Jenaro Herrera (AMNH 278509; MUSM 5531, 5929), Nuevo San Juan (AMNH 272733, 272734; MUSM 13161, 13162, 15158), Quebrada Vainilla (LSUMZ 28424, 28425), Santa Cecilia (FMNH 87030, 89157); see table 38 for measurements.

Unvouchered observations: One individual of *Artibeus lituratus* was captured at Tapiche during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006). Additionally, we caught 16 individuals of *A. lituratus* at El Chino Village between 16 and 21 February 2019.

Identification: *Artibeus lituratus* can be distinguished from other congeners by its large size (forearm >63 mm); brownish dorsal and ventral pelage; ventral pelage without pale frosting; well-defined, bright-white facial stripes; furred dorsal surface of uropatagium; weakly developed hypocone on M1; and by the absence of M3 (Marques-Aguiar, 2008a; López-Baucells et al., 2018). Descriptions and measurements of *A. lituratus* have been provided by Goodwin and Greenhall (1961), Tamsitt and Valdivieso (1966), Swanepoel and Genoways (1979), Davis (1984), Koepcke and Kraft (1984), Handley (1987), Brosset and Charles-Dominique (1990), Lim and Wilson (1993), Marques-Aguiar (1994), Simmons and Voss (1998), Rui et al. (1999), Lim et al. (2005), Marchan-Rivadeneira et al. (2012), and Velazco and Patterson (2019). Two subspecies are currently recognized: *A. l. lituratus* (cis-Andean tropical and subtropical South America from southern Venezuela to northern Argentina) and *A. l. palmarum* (southeastern Mexico south to northern and western Colombia, northern Venezuela, Trinidad and Tobago, and the Lesser Antilles) (Marques-Aguiar, 2008a; Larsen et al., 2013).

FIG. 23. Photographs of **A,** an adult *Artibeus lituratus* captured at Jenaro Herrera; **B,** an adult *A. obscurus* captured at Quebrada Blanco; and **C,** an adult *A. planirostris* captured at El Chino Village. Photographs by Marco Tschapka (A, B) and Brock Fenton (C).

TABLE 38

External and Craniodental Measurements (mm) and Weights (g) of *Artibeus concolor* and *A. lituratus* from the Yavarí-Ucayali Interfluve

	A. concolor		*A. lituratus*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	18.0 (16–20) 4	20, 22	68.1 (60–78) 6	72.5 (67.5–77.5) 5
ToL	61.3 (60–63) 4	72, 60	94.8 (85–101) 6	94.3 (84–104) 6
HF	11.0 (10–12) 4	12, 10	17.9 (13–20) 7	17.8 (16–21) 6
E	18.3 (18–19) 4	18, 19	23.8 (22–25) 6	22.9 (21–25) 6
F	47.7 (46.3–50.4) 4	52.0, 49.0	70.5 (67.5–73.0) 6	71.8 (67.0–75.0) 6
GLS	21.2 (20.7–21.8) 3	21.6, 21.8	30.4 (29.0–31.2) 3	32.1 (31.8–32.4) 4
CIL	19.3 (19.0–19.7) 3	20.5, 20.0	28.0 (27.9–28.1) 2	28.9 (28.7–29.2) 3
PB	5.5 (5.4–5.9) 3	5.9, 6.0	7.0 (6.4–7.2) 3	7.2 (6.9–7.8) 4
BB	10.1 (9.8–10.5) 3	10.0, 9.9	13.5 (13.3–13.6) 3	13.9 (13.6–14.4) 4
MB	11.5 (11.1–12.2) 3	11.2, 11.5	16.6 (15.6–17.2) 3	17.3 (16.9–17.9) 4
ZB	13.5 (12.7–14.4) 2	13.2, 13.7	19.1 (18.9–19.3) 2	20.1 (20.0–20.3) 3
MTL	7.1 (7.0–7.4) 3	7.6, 7.2	10.9 (10.4–11.3) 3	11.7 (11.6–12.0) 4
BAM	9.2 (8.7–9.8) 3	9.5, 9.6	13.4 (12.9–13.7) 3	14.4 (13.9–14.8) 3

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 1321, 5513, 6967, 6970.

[b] MUSM 5514, 6968.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272733, 272734, 278509; FMNH 89157; MUSM 5531, 13161, 15158.

[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 87030; LSUMZ 28424, 28425; MUSM 13162, 32445, 32446.

Ascorra et al. (1993) and Fleck et al. (2002) correctly identified their material from Jenaro Herrera and Nuevo San Juan, respectively, as *Artibeus lituratus*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the nominotypical subspecies, with measurements that fall within the previously documented range of size variation for that taxon.

Remarks: Of 41 nocturnal captures of *Artibeus lituratus* accompanied by ecological data from our region, 22 were made in ground-level mistnets, 18 in elevated nets, and 1 in a harp trap. Of these mistnet and harp-trap captures, 17 were in primary forest, 2 were in secondary vegetation, and 22 were in clearings. The only roost we found of this species was beneath an apparently unmodified frond of *Oenocarpus bataua* (Arecaceae) about 3 m above the ground in primary hilltop forest near Nuevo San Juan; this roost was inhabited by a single adult male that we collected on 11 November 1999. Palm-frond roosts of *Artibeus lituratus* are sometimes modified by biting to provide inconspicuous toeholds (Muñoz-Romo and Herrera, 2003); we cannot rule out the possibility that the frond from which our specimen was collected was similarly modified because we had no opportunity to inspect it closely.

Artibeus (*Artibeus*) *obscurus* (Schinz, 1821)

Figure 23B

Voucher material (total = 26): Estación Biológica Madre Selva (MUSM 32527, 32528), Jenaro Herrera (AMNH 278478; CEBIOMAS 92; MUSM 865, 866), Nuevo San Juan (AMNH

TABLE 39

External and Craniodental Measurements (mm) and Weights (g) of *Artibeus obscurus* and *A. planirostris* from the Yavarí-Ucayali Interfluve

	A. obscurus		*A. planirostris*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	35.7 (30.0–43.5) 12	36.7 (27.0–44.0) 6	52.5 (48–60) 4	—
ToL	77.4 (66–81) 14	77.8 (72–83) 6	91.3 (85–100) 4	90.0 (90–90) 2
HF	15.5 (14–17) 14	14.8 (12–18) 6	16.5 (15–21) 8	16.3 (14–20) 7
E	20.5 (17–24) 14	20.8 (20–22) 6	22.8 (21–24) 4	23.5 (23–24) 2
F	60.1 (57.0–64.0) 13	60.2 (58.0–63.0) 6	67.3 (62.0–71.0) 8	68.3 (65.9–70.3) 7
GLS	27.8 (27.3–28.3) 6	27.4 (26.7–28.1) 5	30.0 (29.5–31.1) 3	30.4 (30.0–30.7) 2
CIL	25.0 (24.3–25.7) 6	24.9 (24.6–25.3) 5	27.6 (27.0–28.7) 3	26.9
PB	6.7 (6.5–6.9) 6	6.8 (6.6–7.0) 5	7.8 (7.7–7.9) 3	7.2 (6.9–7.4) 2
BB	12.3 (11.6–12.6) 6	12.2 (11.6–12.5) 5	13.2 (12.8–13.5) 3	13.3 (13.3–13.4) 2
MB	14.7 (14.3–15.0) 6	14.4 (13.9–15.0) 5	16.6 (16.0–17.1) 3	16.5 (16.2–16.9) 2
ZB	16.7 (16.3–17.3) 6	16.7 (15.9–17.4) 5	18.7 (18.3–18.9) 3	19.6 (19.6–19.6) 2
MTL	10.1 (9.8–10.6) 6	10.1 (9.9–10.4) 5	11.6 (11.3–12.0) 3	11.3 (11.1–11.4) 2
BAM	12.7 (12.3–13.4) 6	12.3 (11.8–12.9) 5	14.0 (13.7–14.5) 3	13.6

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272683, 272753, 272844; CEBIOMAS 92; FMNH 89074; LSUMZ 28426–28428; MUSM 13163, 13166, 13167, 15159, 32527, 32528.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272736, 278478; MUSM 865, 866, 13164, 13165.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272788; CEBIOMAS 93; FMNH 89160; MUSM 4337, 4351, 4352, 5510, 13160.

[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 87028, 87029, 89158; MUSM 4336, 4338, 4350, 4353.

272683, 272736, 272753, 272844; MUSM 13163–13167, 15159), Quebrada Betilia (MUSA 15160, 15171), Quebrada Lobo (MUSA 15117, 15136, 15142), Quebrada Sábalo (MUSA 15211), Quebrada Vainilla (LSUMZ 28426–28428), San Vicente (FMNH 89074); see table 39 for measurements.

Unvouchered observations: Two individuals of *Artibeus obscurus* were captured at Divisor and five at Tapiche during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006). During the Yavarí Rapid Biological Inventory, three individuals were captured at Quebrada Buenavista and one at Quebrada Curacinha (Escobedo, 2003). Additionally, we captured four individuals at Frog Valley on 17 February 2019.

Identification: *Artibeus obscurus* can be easily distinguished from other congeneric species by the following characteristics: medium size (forearm 55–65 mm), dorsal fur blackish and long (8–10 mm), no long guard hairs extending beyond fur surface, facial stripes very pale or absent, and M3 variably present (Haynes and Lee, 2004; Marques-Aguiar, 2008a; López-Baucells et al., 2018). Descriptions and measurements of *A. obscurus* (previously known as *A. fuliginosus*) were provided by Koepcke and Kraft (1984), Handley (1987), Brosset and Charles-Dominique (1990), Lim and Wilson (1993), Marques-Aguiar (1994), Simmons and Voss (1998), Haynes and Lee (2004), Lim et al. (2005), and Velazco and Patterson (2019). No subspecies are currently recognized (Marques-Aguiar, 2008a).

Ascorra et al. (1993) and Fleck et al. (2002) correctly identified their specimens from Jenaro Herrera and Nuevo San Juan, respectively, as *Artibeus obscurus*. The voucher material we examined

from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the range of size variation previously documented for *A. obscurus*.

Remarks: Of 19 recorded nocturnal captures of *Artibeus obscurus* accompanied by ecological data from our region, 18 were in ground-level mistnets and 1 was in an elevated net. Of these mistnet captures, 18 were in primary forest and 1 was in secondary vegetation. The single roosting group that we encountered was in a dark recess between the buttresses of a large fig tree (*Ficus* sp.) about 2 m above the ground in primary upland forest near Nuevo San Juan; two individuals were observed, of which one adult male was collected on 11 November 1999.

The roosting habits of *Artibeus obscurus* remain poorly documented but seem to differ from those of other congeners, which typically roost in foliage. By contrast, *A. obscurus* seems to prefer darker refugia, either beneath exfoliating bark (Simmons and Voss, 1998), inside a cavity in a standing dead tree (Patterson, 1992), or in a deeply shaded recess between tree buttresses (this study). Correspondingly, the pelage of *A. obscurus* is darker than that of most other congeners, and this species lacks the bright-white or whitish facial stripes seen in many foliage-roosting stenodermatines, including most *Artibeus* species.

Artibeus (*Artibeus*) *planirostris* (Spix, 1823)

Figure 23C

Voucher material (total = 19): Isla Padre (MUSM 4336–4338, 4350–4353), Jenaro Herrera (CEBIOMAS 93; MUSM 5510), Nuevo San Juan (AMNH 272788; MUSM 13160), Quebrada Betilia (MUSA 15161, 15172, 15185), Quebrada Esperanza (FMNH 89160), Río Blanco (MUSA 15100), Santa Cecilia (FMNH 87028, 87029, 89158); see table 39 for measurements.

Unvouchered observations: One individual of *Artibeus planirostris* was captured at Tapiche during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006). During the Yavarí Rapid Biological Inventory, one individual of *A. planirostris* was captured at Quebrada Curacinha and another at Quebrada Limera (Escobedo, 2003). At El Chino Village we recorded 34 captures of *A. planirostris* between 16 and 21 February 2019, and we captured one individual at Tahuayo Farm on 19 February 2019.

Identification: The taxonomic status of *Artibeus planirostris* has been the subject of considerable debate. Some authors have treated *planirostris* as a subspecies of *A. jamaicensis* (e.g., Handley, 1987, 1991; Marques-Aguiar, 1994; Simmons and Voss, 1998; Simmons, 2005), whereas others have considered these taxa to be distinct species (e.g., Koepcke and Kraft, 1984; Owen, 1987a; Lim and Wilson, 1993; Lim, 1997; Hollis, 2005; Simmons and Cirranello, 2020). Recent molecular studies based on mitochondrial and nuclear markers support the recognition of *A. jamaicensis* and *A. planirostris* as distinct species (Larsen et al., 2007, 2010a, 2013; Hoofer et al., 2008; Redondo et al., 2008). So recognized, *A. planirostris* occurs throughout most of the rainforested lowlands of cis-Andean South America (Hollis, 2005; Larsen et al., 2010b). This species can be distinguished from other species of *Artibeus* by the following combination of characteristics: large size (forearm 62–73 mm, greatest length of skull 29–33 mm); dorsal fur short (6–8 mm) and dense, with a few long guard hairs extending beyond the fur surface; grayish to gray-brown dorsal and ventral pelage; ventral margin of narial horseshoe separate from upper lip; tubercles on lower lip large, always more than four on each side of chin; facial stripes weakly defined; dorsal surface of uropatagium and legs sparsely haired, appearing naked; preorbital and postorbital processes poorly developed; and breadth across upper molars >14 mm (Hollis, 2005; Marques-Aguiar, 2008a; López-Baucells et al., 2018). Descriptions and measurements of *Artibeus planirostris* (in a variety of binomial and trinomial combinations; see above and below) were provided by Husson (1962, 1978), Patten (1971), Handley (1987), Brosset and Charles-Dominique (1990), Lim and Wilson (1993), Lim

(1997), Hollis (2005), Lim et al. (2005), and Velazco and Patterson (2019).

In addition to differences of opinion about species status, there have also been disagreements concerning the number of subspecies that should be recognized in what is now recognized as *Artibeus planirostris*. Koopman (1978, 1994), Hollis (2005), and Marques-Aguiar (2008a) recognized three: *A. p. fallax* (Venezuela [south and east of the Orinoco]), Trinidad, Grenada, Guyana, Surinam, French Guiana, and the lower Amazon basin of Brazil), *A. p. hercules* (southeastern Colombia and the eastern lowlands of Ecuador, Peru, and Bolivia), and *A. p. planirostris* (southern Bolivia, northern Argentina, Paraguay, and eastern and southern Brazil). Larsen et al. (2007) recognized two additional subspecies: *A. p. grenadensis* (Grenada and St. Vincent and the Grenadines) and *A. p. trinitatis* (Trinidad, Tobago, northern Colombia, and northern Venezuela). The only obvious morphological difference among these taxa is that *A. p. hercules* tends to be larger than other subspecies (Hollis, 2005). However, measurements of our voucher material from the Yavarí-Ucayali interfluve span the entire range of size variation for the species, suggesting that size is not a good feature for delimiting subspecies. Until more comprehensive studies including larger sample sizes and additional data from different molecular markers (e.g., nuclear genes) become available, we recommend against formally recognizing subspecies of *Artibeus planirostris*.

Ascorra et al. (1993) and Fleck et al. (2002) identified their material from Jenaro Herrera and Nuevo San Juan, respectively, as *Artibeus jamaicensis*. Those specimens, together with additional voucher material that we examined from the Yavarí-Ucayali interfluve, agree with currently accepted morphological descriptions of *A. planirostris*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Of 55 recorded nocturnal captures of *Artibeus planirostris* accompanied by ecological information from our region, 44 were made in ground-level mistnets, 9 were made in elevated nets, and 2 were made in harp traps. Ten of these captures were in primary forest, 3 were in secondary vegetation, 40 were in clearings, 1 was in a swampy mineral lick (*collpa*), and 1 was on a river beach. No roosting groups of this species were encountered during our study.

Artibeus (*Dermanura*) *anderseni* Osgood, 1916

Figure 24A

Voucher material (total = 45): Boca Río Yaquerana (FMNH 89057), Estación Biológica Madre Selva (MUSM 32318), Isla Muyuy (MUSM 21001–21009), Isla Padre (MUSM 4210, 4359, 4360), Jenaro Herrera (AMNH 278472; MUSM 1323, 5525, 5537, 6965), Nuevo San Juan (AMNH 272768, 272789, 272790, 272831, 273142, 273143–273145, 273183, 273187; MUSM 13151–13155, 15179–15184), Quebrada Esperanza (FMNH 89058), Quebrada Vainilla (LSUMZ 28436), Santa Cecilia (FMNH 87077–87079); see table 40 for measurements.

Unvouchered observations: One individual of *Artibeus anderseni* was captured at Quebrada Limera during the Yavarí Rapid Biological Inventory (Escobedo, 2003), and we captured another three individuals at El Chino Village.

Identification: Small species of *Artibeus* (all of which belong to the subgenus *Dermanura*) are difficult to identify in the field because many of the external features that have been alleged to differentiate species are intraspecifically variable (Simmons and Voss, 1998). Therefore, a combination of external and craniodental characteristics are necessary for confident identifications. *Artibeus anderseni* can be distinguished from other small *Artibeus* by the following combination of characteristics: pale-brown to grayish dorsal pelage; tricolored dorsal fur; distinct white facial stripes; margins of ear pale yellow or whitish; only proximal half of forearm covered by long, dense fur; uropatagium dark brown and naked (hairless); rostrum short, broad, and elevated (tilted upward); posterior palatal border U-shaped; impression of optic nerve in orbit

FIG. 24. Photographs of **A,** an adult *Artibeus anderseni* and **B,** an adult *A. gnomus*, both captured at Jenaro Herrera. Photographs by Marco Tschapka.

TABLE 40

External and Craniodental Measurements (mm) and Weights (g) of *Artibeus anderseni*, *A. bogotensis*, and *A. cinereus* from the Yavarí-Ucayali Interfluve

	A. anderseni		*A. bogotensis*	*A. cinereus*	
	Males[a]	Females[b]	MUSM 1320 ♀	Males[c]	Females[d]
W	9.1 (8–10) 25	10.6 (8–14) 10	10	9.1 (8–10) 8	9.8 (8–11) 8
ToL	48.3 (40–53) 28	48.9 (45–53) 13	52	51.9 (49–54) 8	53.3 (50–55) 8
HF	8.8 (7–11) 31	9.5 (9–10) 13	9	10.6 (9–11) 9	11.0 (10–12) 8
E	14.7 (12–17) 28	15.4 (15–17) 13	17	14.6 (14–15) 8	15.1 (14–16) 8
F	35.2 (33.0–37.0) 31	35.7 (34.0–37.0) 12	37.0	36.0 (34.2–39.0) 9	36.3 (35.5–38.4) 8
GLS	17.6 (17.0–18.1) 17	17.8 (17.3–18.1) 7	19.1	17.9 (17.6–18.4) 4	17.9 (17.6–18.5) 8
CIL	15.9 (15.2–16.6) 17	15.9 (15.5–16.2) 7	17.1	16.1 (15.9–16.5) 4	16.3 (15.8–16.6) 8
PB	4.5 (4.3–4.7) 17	4.6 (4.3–4.9) 7	4.9	4.6 (4.5–4.8) 4	4.7 (4.5–5.0) 8
BB	8.4 (8.0–8.9) 17	8.4 (8.3–8.6) 7	8.3	8.4 (8.2–8.6) 4	8.6 (8.2–9.1) 8
MB	9.4 (9.0–10.5) 17	9.3 (9.1–9.8) 7	9.8	8.9 (8.6–9.3) 4	9.2 (8.8–9.7) 8
ZB	10.7 (10.2–11.3) 17	10.7 (10.2–10.9) 7	10.7	10.8 (10.4–11.3) 4	11.0 (10.7–11.2) 8
MTL	5.6 (5.1–5.8) 17	5.4 (5.3–5.6) 7	5.9	5.6 (5.3–5.9) 4	5.6 (5.3–5.8) 8
BAM	7.6 (7.4–7.9) 16	7.7 (7.3–7.8) 7	8.0	7.8 (7.2–8.0) 4	7.7 (7.3–8.2) 8

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272768, 272789, 272790, 272831, 273142, 273144, 278472; FMNH 87078, 89057; LSUMZ 28436; MUSM 1323, 4210, 4359, 4360, 5525, 5537, 6965, 13152–13155, 15179, 15183, 21002, 21003, 21005–21009, 32318.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273143, 273145, 273183, 273187; FMNH 87077, 87079, 89058; MUSM 13151, 15180, 15181, 15184, 21001, 21004.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 89134; MUSA 15083, 15153, 15154, 15156, 15173, 15175, 15177, 15258.

[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSA 15147, 15150, 15151, 15155, 15178, 15195, 15199, 15200.

weakly developed; angular process weakly developed, not reaching the level of the condyloid process; second upper premolar caniniform; M1 with broad talon; and m3 absent (Marques-Aguiar, 2008a; Díaz et al., 2016; López-Baucells et al., 2018; Rocha et al., 2018a; Solari, 2019a). Descriptions and measurements of *Artibeus anderseni* were provided by Webster and Jones (1980), Rocha et al. (2018a), and Velazco and Patterson (2019). No subspecies are currently recognized (Marques-Aguiar, 2008a).

Ascorra et al. (1993) and Fleck et al. (2002) correctly identified their specimens from Jenaro Herrera and Nuevo San Juan, respectively, as *Artibeus anderseni*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the range of size variation previously documented for *A. andersoni*.

Remarks: Of 16 recorded nocturnal captures of *Artibeus anderseni* accompanied by ecological data from our region, 13 were made in ground-level mistnets and 3 in elevated nets; of these mistnet captures, 4 were in primary forest, 3 were in secondary vegetation, 4 were in clearings, and 5 were in a swampy mineral lick (*collpa*).

We found six roosts of *Artibeus anderseni*, all of them in foliage, near Nuevo San Juan (table 41). Two roosts were in "boat" tents (sensu Kunz et al., 1994) made from banana leaves about 3–4 m above the ground; two were in tents made from the bananalike leaves of *Heliconia* sp. (Musaceae), probably within 2 m of the ground; one was in an "apical" tent made from the leaf of

TABLE 41

Roosting Groups of *Artibeus anderseni* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
13 Oct 1999	foliage (leaf tent)	6	yes	1 ad. male, 3 ad. females, 2 juv. males
13 Oct 1999	foliage (leaf tent)	3	yes	1 ad. male, 1 ad. female, 1 juv. male
17 Oct 1999	foliage (leaf tent)	2	no	1 ad. female
26 Oct 1999	foliage (leaf tent)	1	yes	1 ad. female
28 Oct 1999	foliage (leaf tent)	1	yes	1 ad. male
29 Oct 1999	foliage (leaf tent)	5	yes	1 ad. male, 2 ad. females, 2 juv. (unsexed)

a hemiepiphyte growing on a *Cecropia* tree at an unrecorded height; and one was in a tent made from the bifid leaf of an understory palm (*Geonoma* sp.). Most roosts were found in secondary vegetation (usually abandoned swiddens), but the palm-leaf roost was in primary hillside forest.

All previously described roosts of this species (Timm, 1987; Díaz and Linares García, 2012) were also in leaf tents.

Artibeus (*Dermanura*) *bogotensis* (Andersen, 1906)

Voucher material (total = 1): Jenaro Herrera (MUSM 1320); see table 40 for measurements.

Unvouchered observations: None.

Identification: *Artibeus bogotensis* was originally described (Andersen, 1906b) as a subspecies of *A. cinereus*. It was subsequently variously treated as a subspecies of *A. cinereus* (e.g., by Andersen, 1906b, 1908; Cabrera, 1958; Koopman, 1994) or *A. glaucus* (e.g., by Handley, 1987; Simmons, 2005; Marques-Aguiar, 2008a), until Lim et al. (2008) raised it to full species rank. *Artibeus bogotensis* can be distinguished from other species in the subgenus *Dermanura* by the following combination of characteristics: pale-brown to grayish dorsal pelage; tricolored dorsal fur; distinct white facial stripes; margins of ear pale cream or whitish; entire forearm covered by long, dense fur; uropatagium dark brown and sparsely furred; rostrum short, slender, and elevated (tilted upward); posterior palatal border V-shaped, with nearly straight sides; impression of optic nerve in orbit well developed; angular process well developed but not reaching the level of the condyloid process; second upper premolar caniniform; M1 with narrow talon; and m3 absent (Handley, 1987; Lim et al., 2008; Calderón and Pacheco, 2012; Solari, 2019b). Descriptions and measurements of *A. bogotensis* have been provided by Andersen (1906b, 1908), Handley (1987), Lim et al. (2005), Lim et al. (2008), and Calderón and Pacheco (2012). No subspecies are currently recognized (Lim et al., 2008).

Ascorra et al. (1993) identified the specimen from Jenaro Herrera as *Artibeus gnomus*, but Calderón and Pacheco (2012) subsequently reidentified it as *A. bogotensis*, an assessment with which we concur. This specimen is the only record of the species in Peru.

Remarks: No ecological information accompanies the single recorded capture of *Artibeus bogotensis* from our region.

Artibeus (*Dermanura*) *cinereus* (Gervais, 1856)

Voucher material (total = 17): Quebrada Betilia (MUSA 15150, 15151, 15153–15156, 15173, 15175, 15177, 15178, 15195, 15199, 15200), Quebrada Lobo (MUSA 15147), Quebrada Pantaleón (MUSA 15258), Río Blanco (MUSA 15083), Santa Cecilia (FMNH 89134); see table 40 for measurements.

TABLE 42

External and Craniodental Measurements (mm) and Weights (g) of *Artibeus glaucus* and *A. gnomus* from the Yavarí-Ucayali Interfluve

	A. glaucus		*A. gnomus*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	11, 10.5	10.7 (8–12) 3	10.6 (9–16) 9	11.0 (9–15) 8
ToL	51, 50	54.0 (52–56) 3	50.2 (48–55) 9	53.3 (49–59) 8
HF	11, 10	8.3 (8–9) 3	8.8 (8–11) 9	9.5 (8–11) 8
E	16, 16	16.0 (15–17) 3	15.7 (14–17) 9	16.5 (16–17) 8
F	39.0, 39.0	39.2 (38.0–40.5) 3	38.6 (37.0–41.0) 9	37.7 (36.0–40.0) 8
GLS	–, 18.5	18.5 (18.1–18.8) 3	18.4 (17.9–19.0) 9	18.4 (17.9–18.9) 7
CIL	–, 16.6	16.9 (16.8–17.1) 3	16.9 (16.5–17.5) 9	16.9 (16.5–17.4) 7
PB	5.0, 4.9	5.0 (4.9–5.1) 3	4.9 (4.8–5.2) 9	4.9 (4.7–5.1) 7
BB	–, 8.6	8.6 (8.5–8.7) 3	8.5 (8.2–8.7) 9	8.4 (8.1–8.9) 7
MB	–, 9.7	10.0 (9.8–10.1) 3	9.7 (9.5–10.0) 9	10.0 (9.8–10.2) 7
ZB	10.9, 10.7	10.9 (10.7–11.1) 2	10.7 (10.4–10.9) 8	10.9 (10.4–11.2) 7
MTL	5.9, 5.6	5.8 (5.7–5.9) 3	5.7 (5.5–6.0) 9	5.8 (5.5–5.9) 7
BAM	7.5, 7.4	7.7 (7.6–7.8) 3	7.7 (7.5–8.1) 9	7.7 (7.5–7.9) 7

[a] AMNH 272823, 13157.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 5516, 5518, 21012.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272861; MUSM 861, 5519, 5535, 5590, 5592, 5593, 13156, 21013.
[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272862; CEBIOMAS 91; MUSM 1322, 5591, 13158, 13159, 21014, 21015.

Unvouchered observations: None.

Identification: *Artibeus cinereus* can be distinguished from other small *Artibeus* by the following combination of characteristics: grayish to brownish dorsal pelage; tetracolored (four-banded) dorsal fur; distinct white facial stripes; margins of ear pale cream or whitish; entire forearm covered by long, dense fur; uropatagium blackish and naked (hairless); rostrum short, broad, not elevated, and lacking a dorsal concavity; posterior border of hard palate V-shaped, with nearly straight sides; impression of optic nerve in orbit well developed; angular process well developed and reaching the level of the condyloid process; second upper premolar noncaniniform; M1 with narrow talon; and m3 absent (Marques-Aguiar, 2008a; Díaz et al., 2016; Rocha et al., 2018a; Arroyo-Cabrales, 2019). Descriptions and measurements of *A. cinereus* were provided by Andersen (1908), Husson (1962, 1978), Davis (1970), Swanepoel and Genoways (1979), Webster and Jones (1980), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), and Scultori et al. (2009b). Two subspecies are currently recognized: *A. c. cinereus* (Amazon basin and eastern Brazil) and *A. c. quadrivittatus* (Venezuela, the Guianas, and northern Brazil) (Marques-Aguiar, 2008a).

Medina et al. (2015) correctly identified their material from Quebrada Betilia, Quebrada Lobo, and Quebrada Pantaleón as *Artibeus cinereus*. All the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the nominotypical subspecies, with measurements that fall within the range of size variation previously documented for that taxon.

Remarks: No ecological information is currently available for specimens of *Artibeus cinereus* collected in our region.

Artibeus (*Dermanura*) *glaucus* Thomas, 1893

Voucher material (total = 6): Jenaro Herrera (MUSM 5516, 5518), Nuevo San Juan (AMNH 272823; MUSM 13157), Quebrada Betilia (MUSA 15174), Quebrada Blanco (MUSM 21012); see table 42 for measurements.

Unvouchered observations: None.

Identification: *Artibeus glaucus* is often confused with *A. gnomus*, but it can be distinguished from that species and other congeners by the following combination of characteristics: dark-gray to blackish dorsal pelage; tricolored dorsal fur; weakly defined white facial stripes; ear uniformly pigmented, without distinctly paler margins; entire forearm covered by long, dense fur; uropatagium dark gray and sparsely furred; rostrum short, broad, and not upturned, but with a dorsal concavity in the nasal region; posterior border of hard palate U-shaped; angular process well-developed and reaching the level of the condyloid process; second upper premolar caniniform; M1 with narrow talon; and m3 present (Handley, 1987; Marques-Aguiar, 2008a; Díaz et al., 2016; López-Baucells et al., 2018; Solari, 2019c). Descriptions and measurements of *A. glaucus* were provided by Andersen (1908), Davis (1970), Carter and Dolan (1978), Swanepoel and Genoways (1979), Lim et al. (2008), and Velazco and Patterson (2019). No subspecies are currently recognized (Lim et al., 2008).

Ascorra et al. (1993) identified their specimens from Jenaro Herrera as *Artibeus gnomus*, but after reviewing these specimens we reidentified them as *A. glaucus*. Fleck et al. (2002) and Medina et al. (2015), however, correctly identified their specimens from Nuevo San Juan and Quebrada Betilia, respectively, as *A. glaucus*. All the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the previously documented range of intraspecific size variation.

Remarks: Both individuals of *Artibeus glaucus* from Nuevo San Juan (the only specimens accompanied by ecological data from our region) were collected at roosts. One roost was an unmodified dead palm frond that had fallen from the canopy and was suspended horizontally about 2 m above the ground in the undergrowth of hillcrest primary forest; a single adult male was found clinging to the rachis of this frond on 30 June 1998. A second roost, encountered on the same date, was an unmodified frond of a stemless palm in the understory of primary hillcrest forest; dead leaves had accumulated on the upper surface of the frond, creating a dark place on the underside, which was occupied by two bats (of which one adult male was collected).

Artibeus (*Dermanura*) *gnomus* Handley, 1987

Figure 24B

Voucher material (total = 27): Jenaro Herrera (CEBIOMAS 91; MUSM 861, 1322, 5519, 5535, 5590–5593, 6969), Nuevo San Juan (AMNH 272861, 272862; MUSM 13156, 13158, 13159), Quebrada Betilia (MUSA 15152), Quebrada Blanco (MUSM 21013–21015), Quebrada Lobo (MUSA 15120, 15122), Quebrada Pantaleón (MUSA 15244, 15245), Quebrada Sábalo (MUSA 15213, 15216), Río Blanco (MUSA 15104, 15105); see table 42 for measurements.

Unvouchered observations: None.

Identification: *Artibeus gnomus* can be distinguished from other small *Artibeus* by the following combination of traits: pale-brown to grayish-brown dorsal pelage; tricolored dorsal fur; distinct white facial stripes; margins of ear yellow; only proximal half of forearm covered by long and dense fur; uropatagium brown and naked (hairless); rostrum short, broad, not elevated, and lacking a dorsal concavity; posterior border of hard palate V-shaped, with nearly straight sides; impression of optic nerve in orbit well developed; angular process weakly developed and not reaching the level of the condyloid process; second upper premolar caniniform; M1 with broad talon; and m3 present (Handley, 1987; Marques-Aguiar, 2008a; Dávalos et al., 2014; Díaz et al., 2016; Solari, 2019d). Descriptions and

measurements of *Artibeus gnomus* have been provided by Handley (1987), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), and Lim et al. (2005). No subspecies are currently recognized (Marques-Aguiar, 2008a).

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their specimens from Jenaro Herrera, Nuevo San Juan, Quebrada Betilia, Quebrada Lobo, Quebrada Pantaleón, and Quebrada Sábalo as *Artibeus gnomus*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the previously documented range of size variation for *A. gnomus*.

Remarks: Only six recorded nocturnal captures of *Artibeus gnomus* from our region are accompanied by ecological information. Of these, 5 were made in ground-level mistnets, and 1 was made in an elevated net. Five of these mistnet captures were in primary forest, but one was in secondary vegetation.

We encountered two roosts of this species, both of which were "apical" tents (sensu Kunz et al., 1994) made from leaves of hemiepiphytic aroids (probably *Philodendron* sp.). The first was about 6 m above the ground on the trunk of a *Cecropia* tree in secondary vegetation near Nuevo San Juan on 8 July 1998 (a field drawing of this roost was reproduced by Simmons and Voss, 2009: fig. 42.2); this shelter was occupied by one adult male and three adult females, all of which were collected. The second roost was only about 2 m above the ground in secondary vegetation at Jenaro Herrera on 29 January 2012; this tent was occupied by three or four bats, of which only one adult female was collected.

Genus *Chiroderma* Peters, 1860

The genus *Chiroderma* includes seven currently recognized species that can be distinguished from other stenodermatines by the following combination of characteristics: muzzle short, broad, and deep; dorsal fur dense, with long guard hairs standing out above the underfur covering the body, and especially conspicuous on the cephalic region; legs furred; uropatagium partially furred but lacking a conspicuous fringe of hair on its trailing edge; horseshoe of noseleaf with free margins along its entire extension; eyes large; skull with a conspicuous notch at the region of the nasal bones, which are extremely reduced; large orbital region; hard palate long, extending posteriorly almost to the glenoid fossa; inner upper incisors long and pointed; first upper premolar and canine in contact; and first and second upper premolars lacking hypocones (Emmons and Feer, 1997; Gardner, 2008e; Taddei and Lim, 2010; Garbino et al., 2020). We recorded both species of *Chiroderma* expected to occur in the Yavarí-Ucayali interfluve following the revised distributional data in Garbino et al. (2020).

Chiroderma trinitatum Goodwin, 1958

Figure 25A

Voucher material (total = 9): Jenaro Herrera (AMNH 278477; MUSM 4219, 5594), Quebrada Betilia (MUSA 15167), Quebrada Esperanza (FMNH 89083, 89085, 89093), Quebrada Lobo (MUSA 15128), Río Blanco (MUSA 15101); see table 43 for measurements.

Unvouchered observations: One individual of *Chiroderma trinitatum* was captured at Tapiche during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006).

Identification: *Chiroderma trinitatum* is distinguished from other congeneric species by its small size (forearm <43 mm, greatest length of skull <23 mm); conspicuous white facial and middorsal stripes; and inner upper incisors that converge only distally, contacting each other at the tips (Gardner, 2008e; Garbino et al., 2012, 2020; López-Baucells et al., 2018). Descriptions and measurements of *C. trinitatum* were provided by Goodwin (1958), Goodwin and Greenhall (1961), Ojasti and Linares (1971), Baker and Genoways (1976), Gardner (1976), Carter and Dolan (1978), Bergmans (1979), Genoways and Williams (1979), Swanepoel and Genoways (1979), Brosset and Charles-Dominique

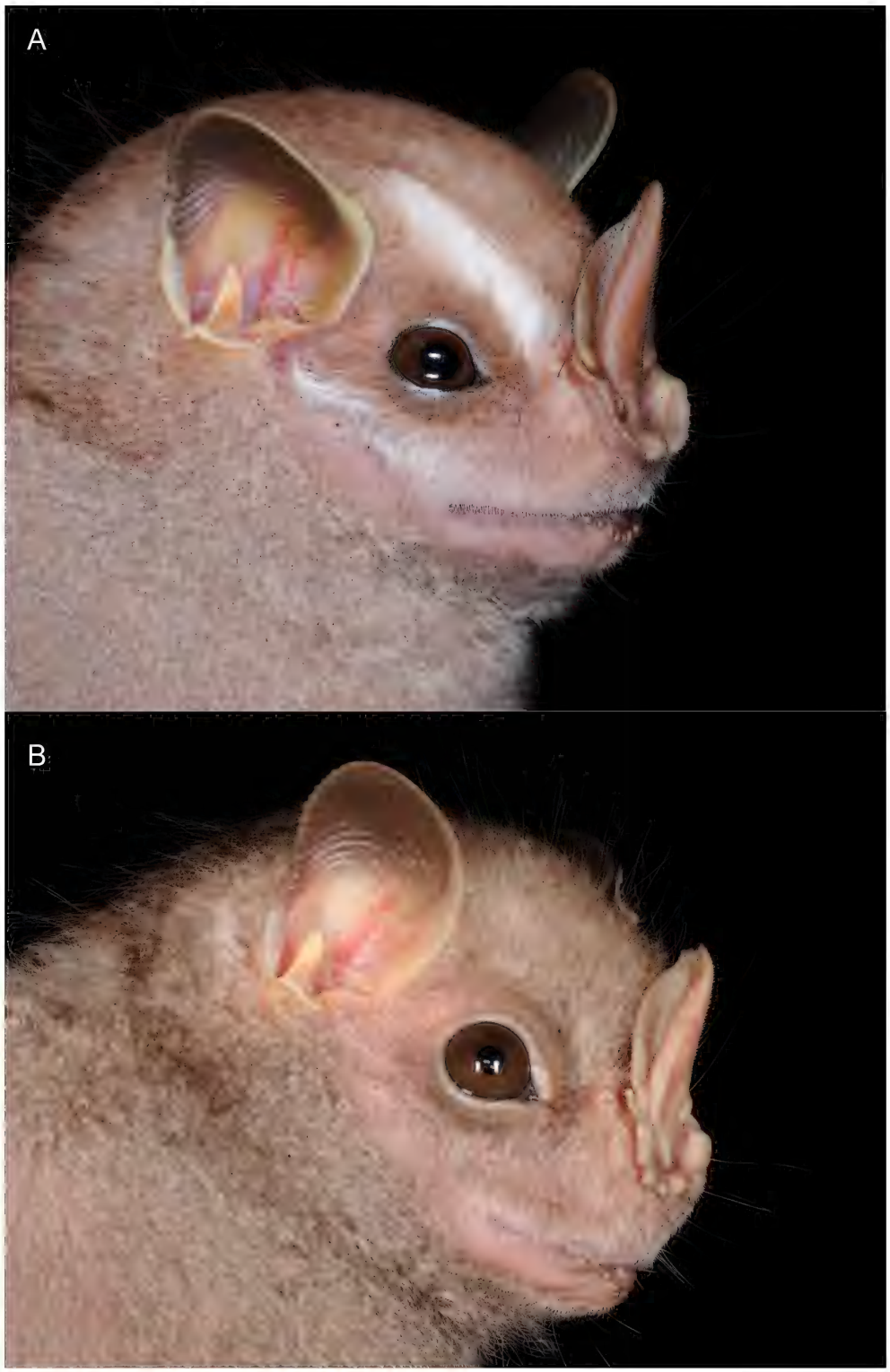


FIG. 25. Photographs of **A,** an adult *Chiroderma trinitatum* and **B,** an adult *C. villosum*, both captured at Jenaro Herrera. Photographs by Marco Tschapka.

TABLE 43

External and Craniodental Measurements (mm) and Weights (g) of *Chiroderma* from the Yavarí-Ucayali Interfluve

	C. trinitatum		*C. villosum*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	13.4 (13–15) 4	14.9	18	23, 27.5
ToL	57.0 (53–60) 6	61.3 (60–64) 3	66.3 (62–69) 3	72.0 (70–75) 3
HF	10.8 (9–13) 6	12.3 (11–13) 3	12.2 (11–13) 4	12.5 (11–14) 4
E	15.9 (14–18) 6	17.1 (16–18) 3	18.0 (18–18) 3	18.0 (17–19) 3
F	39.5 (38.0–40.7) 6	41.1 (41.0–41.2) 3	45.9 (44.8–47.0) 4	47.6 (46.0–50.0) 4
GLS	21.0 (20.7–21.4) 6	21.8 (21.4–22.3) 3	24.1 (23.6–24.4) 4	24.8 (24.0–25.2) 3
CIL	19.3 (18.6–19.6) 5	19.8 (19.4–20.2) 3	22.0 (21.8–22.3) 4	22.1 (21.4–22.7) 3
PB	5.2 (5.0–5.4) 6	5.4 (5.2–5.5) 3	5.8 (5.7–5.9) 4	5.8 (5.7–6.0) 3
BB	9.4 (9.3–9.7) 6	9.7 (9.5–9.8) 3	10.9 (10.5–11.6) 4	10.9 (10.7–11.2) 3
MB	10.5 (10.2–10.9) 6	10.7 (10.3–11.1) 3	12.1 (12.0–12.2) 4	12.3 (12.0–12.6) 3
ZB	13.0 (12.6–13.2) 6	13.3 (12.8–13.5) 3	15.4 (14.9–15.8) 4	16.0 (15.7–16.4) 3
MTL	7.1 (6.9–7.3) 5	7.2 (7.0–7.4) 3	8.7 (8.6–8.9) 4	9.1 (8.8–9.4) 3
BAM	9.4 (9.2–9.8) 5	9.5 (9.4–9.6) 3	11.0 (10.9–11.2) 4	11.5 (11.3–11.9) 3

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 278477; FMNH 89093; MUSA 15101, 15128; MUSM 4219, 5594.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 89083, 89085; MUSA 15167.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 89079, 89080; MUSM 4222, 6971.

[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of CEBIOMAS 97; FMNH 87035; MUSM 4221, 32809.

(1990), Simmons and Voss (1998), Lim et al. (2005), Taddei and Lim (2010), Garbino et al. (2012), Tello et al. (2014), Rocha et al. (2016), and Velazco and Patterson (2019). No subspecies are currently recognized (Garbino et al., 2020).

Ascorra et al. (1993), Tello et al. (2014), and Medina et al. (2015) correctly identified their material from Jenaro Herrera, Quebrada Betilia, Quebrada Lobo, and Río Blanco as *Chiroderma trinitatum*. The additional voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the species, with measurements that fall within the previously documented range of intraspecific size variation. One specimen from Jenaro Herrera (MUSM 4219) represents the first case of leucism for the species (Tello et al., 2014).

Remarks: Five recorded captures of *Chiroderma trinitatum* accompanied by ecological data from our region include three made in ground-level mistnets and two in elevated nets; of these, one capture was made in primary forest and four were made in clearings. No roosting groups of this species were encountered during our study, although it seems likely that the specimens collected by C. Kalinowski at Quebrada Esperanza may have come from a roost.

Chiroderma villosum Peters, 1860

Figure 25B

Voucher material (total = 15): Estación Biológica Madre Selva (MUSM 32809); Jenaro Herrera (CEBIOMAS 97; MUSM 4221, 4222,

6971), Quebrada Betilia (MUSA 15149), Quebrada Esperanza (FMNH 89079, 89080), Quebrada Lobo (MUSA 15146), Río Blanco (MUSA 15066, 15074, 15079, 15097, 15098), Santa Cecilia (FMNH 87035); see table 43 for measurements.

Unvouchered observations: Four individuals of *Chiroderma villosum* were captured at El Chino Village on 21 February 2019.

Identification: *Chiroderma villosum* is easily distinguished from other species in the genus by the following combination of characteristics: medium size (forearm >40 mm, greatest length of skull >23 mm); pale facial and dorsal stripes inconspicuous or absent; and upper inner incisors slender and parallel (not convergent) (Gardner, 2008e; López-Baucells et al., 2018; Garbino et al. 2020). Descriptions and measurements of *C. villosum* were provided by Goodwin and Greenhall (1961), Husson (1962, 1978), Hill (1964), Ceballos-Bendezú (1968), Baker and Genoways (1976), Carter and Dolan (1978), Genoways and Williams (1979), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Lim et al. (2005), Taddei and Lim (2010), Garbino et al. (2012), and Rocha et al. (2016 [who reported Brazilian specimens misidentified as *C. salvini*]). Two subspecies are currently recognized: *C. v. jesupi* (western Mexico to northwestern Peru and northern Colombia) and *C. v. villosum* (east of the Andes in tropical South America) (Gardner, 2008e; Garbino et al. 2020).

Ceballos-Bendezú (1968), Ascorra et al. (1993), and Medina et al. (2015) correctly identified their material from Quebrada Esperanza, Jenaro Herrera, Quebrada Lobo, and Río Blanco as *Chiroderma villosum*. Medina et al. (2015) erroneously reported an adult female specimen from Quebrada Betilia (MUSA 15149) as *Chiroderma salvini*, but Garbino et al. (2020) correctly identified that specimen as *C. villosum*. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of the nominotypical subspecies, with measurements that fall within the range of size variation previously documented for that taxon.

Remarks: Of six specimens of *Chiroderma villosum* accompanied by capture data from our region, two were taken in ground-level mistnets and four in elevated nets; all of these specimens were captured in clearings. No roosting groups of this species were encountered during our study.

Enchisthenes hartii (Thomas, 1892)

Voucher material (total = 1): Jenaro Herrera (MUSM 6966); see table 44 for measurements.

Unvouchered observations: *Enchisthenes hartii* was captured and identified at Quebrada Buenavista (one individual) and Quebrada Limera (two individuals) during the Yavarí Rapid Biological Inventory (Escobedo, 2003).

Identification: *Enchisthenes* contains a single species that is widespread from north-central Mexico to southern Bolivia and eastern Venezuela; there is also an extralimital record from Arizona in the United States, although this individual may have been accidentally imported (Irwin and Baker, 1967; Arroyo-Cabrales and Owen, 1996, 1997; Simmons, 2005; Marques-Aguiar, 2008b). *Enchisthenes hartii* can be distinguished from other stenodermatines by the combination of the following characteristics: small size (forearm 36–42 mm); dark chocolate-brown dorsal fur and paler ventral fur; noseleaf about as long as wide; lower margin of noseleaf horseshoe merged with the upper lip; uropatagium narrow, with a hairy outer edge; inner upper incisors pointed (not bifid); M1 with a slightly to moderately developed hypocone; and M3 relatively large and aligned directly behind M2 (Arroyo-Cabrales and Owen, 1996, 1997; Marques-Aguiar, 2008b; López-Baucells et al., 2018). Descriptions and measurements of *E. hartii* were provided by Gardner (1976), Swanepoel and Genoways (1979), Ascorra et al. (1993), Arroyo-Cabrales and Owen (1996, 1997), Cervantes et al. (2004), and Marques-Aguiar (2008b). No subspecies are currently recognized (Arroyo-Cabrales and Owen, 1996; Marques-Aguiar, 2008b).

TABLE 44

External and Craniodental Measurements (mm) and Weights (g) of *Enchisthenes hartii* and *Mesophylla macconnelli* from the Yavarí-Ucayali Interfluve

	E. hartii	*M. macconnelli*	
	MUSM 6966 ♂	Males[a]	Females[b]
W	16	6.6 (5.0–7.4) 14	7.6 (5.0–10.9) 13
ToL	57	45.0 (39.5–48.0) 21	46.4 (42–51) 20
HF	9	8.9 (7–10) 21	9.1 (7–11) 20
E	16	14.2 (12–16) 21	14.3 (12–16) 20
F	39.3	30.3 (28.0–32.0) 20	31.5 (30.0–33.0) 20
GLS	20.4	17.3 (16.8–18.1) 13	17.5 (16.7–18.2) 14
CIL	19.2	15.7 (15.2–16.1) 14	15.9 (15.4–16.2) 10
PB	5.7	4.4 (4.2–4.7) 15	4.4 (4.3–4.7) 14
BB	9.6	7.8 (7.5–8.1) 14	7.8 (7.6–8.2) 12
MB	10.5	8.8 (8.5–9.1) 13	8.9 (8.6–9.2) 12
ZB	12.7	9.9 (9.6–10.3) 9	10.1 (9.9–10.5) 13
MTL	7.2	5.9 (5.7–6.1) 15	6.0 (5.6–6.3) 14
BAM	8.5	6.9 (6.6–7.3) 16	7.0 (6.5–7.4) 13

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74100, 272725, 272745, 273162, 278480; CEBIOMAS 104; FMNH 87085, 87087–87091, 87094; LSUMZ 28441, 28442, 28444; MUSM 5545, 5935, 13206–13208, 15185, 15187.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272824, 273035, 273049, 273076, 278494; CEBIOMAS 103; FMNH 87086, 87092, 87093, 87095, 87096, 89052; LSUMZ 28443; MUSM 5498, 5936, 5941, 13209, 15186, 15188, 15189.

Ascorra et al. (1993) identified the specimen from Jenaro Herrera as *Artibeus hartii* (the binomen by which this species was previously known). That unique specimen conforms to previous descriptions of *Enchisthenes hartii*, with measurements that fall within the previously documented range of intraspecific size variation.

Remarks: According to Escobedo (2003), the captures of *Enchisthenes hartii* from Quebrada Buenavista and Quebrada Limera were made in seasonally flooded forest, and at least one individual was mistnetted 10 m above the ground near a fruiting fig (*Ficus insipida*) tree. No other ecological information about this species is currently available from our region.

Mesophylla macconnelli (Thomas, 1901)

Voucher material (total = 54): Boca Río Yaquerana (FMNH 89052), Jenaro Herrera (AMNH 278480, 278494; CEBIOMAS 103, 104; MUSM 5498, 5545, 5935, 5936, 5941), Nuevo San Juan (AMNH 272725, 272745, 272824, 273035, 273049, 273076, 273077, 273162; MUSM 13206–13209, 15185–15189), Orosa (AMNH 74100), Quebrada Betilia (MUSA 15183, 15184, 15188, 15201), Quebrada Lobo (MUSA 15107, 15109, 15115, 15121), Quebrada Sábalo (MUSA 15209), Quebrada Vainilla (LSUMZ 28441–28444), Río Blanco (MUSA 15090), Santa Cecilia (FMNH 87085–87096); see table 44 for measurements.

Unvouchered observations: None.

Identification: *Mesophylla* contains a single species that is widespread from southeastern Nicaragua to northern Bolivia and central Brazil (Arroyo-Cabrales, 2008a; Reid, 2009). The taxonomic status of this bat has been debated for most of the second half of the last century. Whereas some authors considered *Mesophylla* to

TABLE 45

Roosting Groups of *Mesophylla macconnelli* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
21 May 1998	foliage (leaf tent)	1	yes	1 ad. male
11 Jun 1998	foliage (leaf tent)	1	yes	1 ad. male
30 Jun 1998	foliage (leaf tent)	3	no	1 ad. female
3 Jul 1998	foliage (leaf tent)	2	no	1 ad. male
9 Jul 1998	foliage (leaf tent)	3?	no	1 ad. female
2 Sep 1999	foliage (leaf tent)	4	no	1 ad. male, 2 ad. females
4 Sep 1999	foliage (leaf tent)	2	yes	1 ad male, 1 ad. female
4 Sep 1999	foliage (leaf tent)	4?	no	1 ad. female
10 Sep 1999	foliage (leaf tent)	3	yes	1 ad. male, 1 ad. female, 1 juv. male
22 Sep 1999	foliage (leaf tent)	2	no	1 ad. female
19 Oct 1999	foliage (leaf tent)	1	yes	1 ad. male
25 Oct 1999	foliage (leaf tent)	2	yes	1 ad. male, 1 ad. female

be a valid genus (e.g., Kunz and Pena, 1992; Koopman, 1993, 1994), others treated it as a junior synonym either of *Ectophylla* (e.g., Goodwin and Greenhall, 1962; Handley, 1976; Koopman, 1978; Simmons and Voss, 1998) or of *Vampyressa* (e.g., Owen, 1987b). Recent molecular studies and subsequent classifications, however, have consistently supported the recognition of *Mesophylla* as a valid genus (e.g., Baker et al., 2000, 2003, 2016; Cirranello et al., 2016; Simmons and Cirranello, 2020). *Mesophylla macconnelli* can be distinguished from other stenodermatines by its small size (forearm 28–34 mm); yellow ears and noseleaf (in live individuals, but paler in museum specimens); small accessory noseleaf-like structure behind the noseleaf; unfurred uropatagium; short skull with a relatively short and narrow rostrum; palate extending well behind the last molars; inner upper incisors long, convergent, and usually with weakly bifid tips; m2 lacking a posterior cuspulid; and minute m3 (Arroyo-Cabrales, 2008a; López-Baucells et al., 2018). Descriptions and measurements of *M. macconnelli* were provided by Goodwin and Greenhall (1962), Ceballos-Bendezú (1968), Starrett and Casebeer (1968), Carter and Dolan (1978), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), and Velazco and Patterson (2019). No subspecies are currently recognized (Arroyo-Cabrales, 2008a).

Ceballos-Bendezú (1968) and Fleck et al. (2002) identified specimens from Boca Río Yaquerana and Nuevo San Juan, respectively, as *Ectophylla macconnelli*, and Ascorra et al. (1993) identified his specimens from Jenaro Herrera as *Vampyressa macconnelli*. All the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Mesophylla macconnelli*, with measurements that fall within the range of size variation previously documented for this species.

Remarks: Of 11 recorded nocturnal captures of *Mesophylla macconnelli* accompanied by ecological information from our region, 10 were made in ground-level mistnets and 1 was in an elevated net. Six mistnet captures were made in primary forest, two in secondary vegetation, and three in clearings.

We found 12 roosts of *Mesophylla macconnelli* (table 45), all of them in understory palm-leaf tents near Nuevo San Juan. Ten roosts were

made from the bifid leaves of dwarf palms (*Geonoma* sp. or *Hyospathe* sp.), but two were made from the undivided terminal leaflets of immature *Attalea butyracea* fronds (mature plants of this species are tall trees with completely pinnate leaves). All roosts were in primary upland forest (on hillcrests, hill slopes, or in well-drained valley bottoms) at recorded heights of 1.0–1.5 m above the ground. We never found *M. macconnelli* sharing a roost with other species of bats.

Most roosts of this species have previously been reported in tents made from the bifid terminal leaflets of palms of the genus *Astrocaryum*, although the leaves of other monocots are also known to be used (Koepcke, 1984; Simmons and Voss, 1998). Our observations from Nuevo San Juan suggest that roost choice of this widespread Amazonian bat may be geographically variable, perhaps in response to differing availability of palm taxa.

Genus *Platyrrhinus* Saussure, 1860

The genus *Platyrrhinus* is a widely distributed Neotropical genus that includes 19 currently recognized species (Palacios-Mosquera et al., 2020). Species of *Platyrrhinus* can be distinguished from other stenodermatines by the following combination of characteristics: presence of a fringe of hair along the trailing margin of the uropatagium; facial and dorsal stripes present; rostrum approximately as wide as, and almost as long as the braincase; large inner upper incisors that are convergent at the tips; upper outer incisors bifid, less than half the length of inner incisors; two accessory cusps on the posterior face of the second upper premolar; and presence of three upper and lower molars (Gardner, 2008f; Velazco and Lim, 2014). Velazco and Gardner (2009) and Velazco et al. (2010a) provided key to the species of *Platyrrhinus* based on external and craniodental characters. All five species expected to occur in the Yavarí-Ucayali interfluve are represented among the specimens we examined.

Platyrrhinus angustirostris Velazco et al., 2010

Voucher material (total = 2): Jenaro Herrera (MUSM 5500, 5928); see table 46 for measurements.

Unvouchered observations: None.

Identification: *Platyrrhinus angustirostris* can be distinguished from conspecific species by the following characteristics: long, dense fur on dorsal surface of feet; U-shaped posterior margin of uropatagium; metacarpal V shorter than metacarpal III; fossa on the squamosal root of the zygomatic arch shallow; three cuspules on posterior cristid of the second upper premolar; M1 protocone well developed; stylar cuspule absent on lingual face of M2 paracone; and m2 hypoconid absent (Velazco et al., 2010a). Descriptions and measurements of *P. angustirostris* were provided by Velazco et al. (2010a) and Velazco and Lim (2014). No subspecies are currently recognized (Velazco et al., 2010a).

Ascorra et al. (1993) identified their specimens from Jenaro Herrera as *Platyrrhinus helleri*, but we reidentified them as *P. angustirostris*.

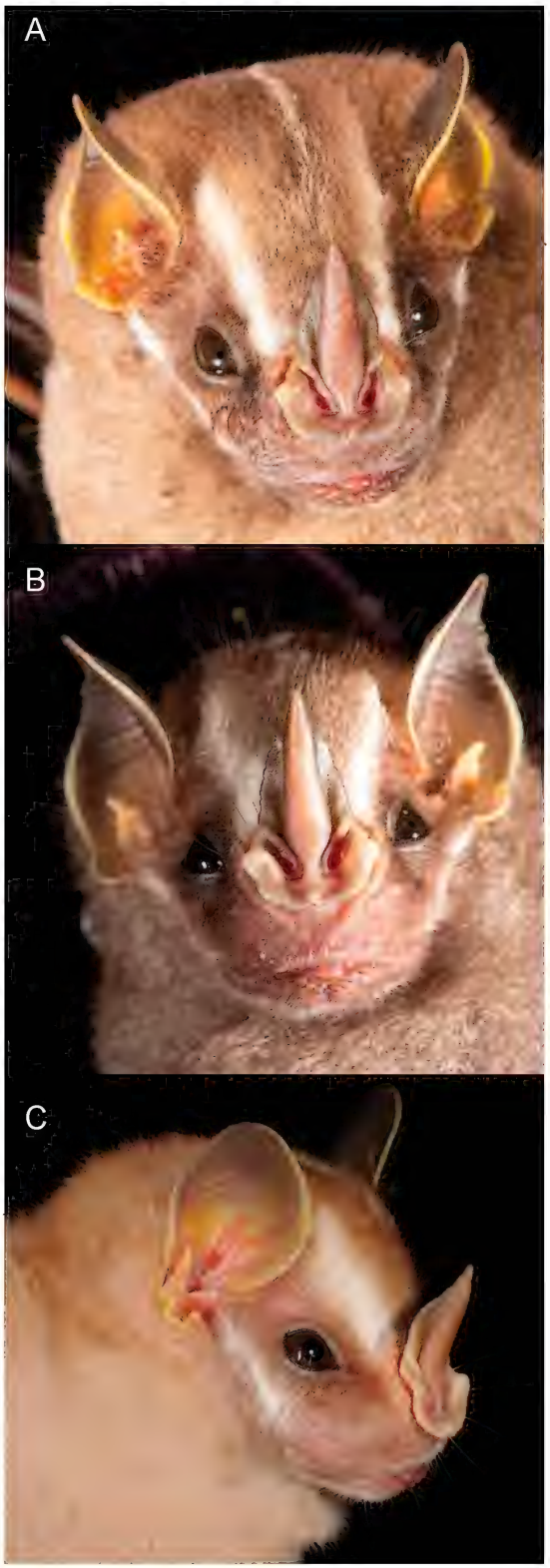
Remarks: No ecological data accompanies either specimen we examined.

Platyrrhinus brachycephalus (Rouk and Carter, 1972)

Figure 26A

Voucher material (total = 16): Estación Biológica Madre Selva (MUSM 32847, 32875), Isla Muyuy (MUSM 21222), Isla Padre (MUSM 4211, 4213, 4361), Jenaro Herrera (MUSM 5927), Quebrada Betilia (MUSA 15166), Quebrada Esperanza (FMNH 89095), Quebrada Lobo (MUSA 15113), Quebrada Pantaleón (MUSA 15253), Orosa (AMNH 73990–73993, 74013); see table 46 for measurements.

Unvouchered observations: One individual of *Platyrrhinus brachycephalus* was captured at Tapiche during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006), and we captured one individual at El Chino Village on 16 February 2019.



Platyrrhinus fusciventris Velazco et al., 2010

Figure 26B

Voucher material (total = 4): Jenaro Herrera (MUSM 871, 4217, 5526, 5598); see table 46 for measurements.

Unvouchered observations: We captured three individuals of *Platyrrhinus fusciventris* at El Chino Village on 16 and 18 February 2019.

Identification: *Platyrrhinus fusciventris* is distinguished from other species in the genus by the following combination of characteristics: short and only moderately dense hair on the dorsal surface of feet; V-shaped notch in posterior margin of uropatagium; metacarpal III subequal to metacarpal V; fossa on the squamosal root of the zygomatic arch shallow; two cuspules on posterior cristid of the second upper premolar; M1 protocone well developed; stylar cuspule absent on lingual face of M2 paracone; and m2 hypoconid absent (Velazco et al., 2010a; López-Baucells et al., 2018). Descriptions and measurements of *P. fusciventris* were provided by Velazco et al. (2010a), Velazco and Lim (2014), and Rocha et al. (2018b). No subspecies are currently recognized (Velazco et al., 2010a).

Ascorra et al. (1993) identified two specimens (MUSM 871, 5526) from Jenaro Herrera as *Platyrrhinus helleri*, but we reidentified them as *P. fusciventris*. The voucher material we examined conforms to previous descriptions of the species, with measurements that fall within the range of size variation previously documented for *P. fusciventris*.

Remarks: The only specimens of *Platyrrhinus fusciventris* accompanied by capture information from our region were taken in clearings and gardens around El Chino Village: two in ground-level mistnets and one in a harp trap.

FIG. 26. Photographs of **A,** an adult *Platyrrhinus brachycephalus* captured at El Chino Village; **B,** an adult *P. fusciventris* captured at El Chino Village; and **C,** an adult *P. incarum* captured at Jenaro Herrera. Photographs by Brock Fenton (A, B) and Marco Tschapka (C).

TABLE 46

External and Craniodental Measurements (mm) and Weights (g) of *Platyrrhinus angustirostris*, *P. brachycephalus*, and *P. fusciventris* from the Yavarí-Ucayali Interfluve

	P. angustirostris	*P. brachycephalus*		*P. fusciventris*
	Males[a]	Males[b]	Females[c]	Females[d]
W	16, 14	12.8 (12–14) 3	13	14, 20
ToL	57, 60	57.7 (55–60) 3	57, 58	52, 54
HF	9, 10	10.5 (9–12) 6	8, 11	8.3 (8–9) 3
E	17, 11	15.3 (15–16) 3	16, 16	16, 17
F	39.0, 39.5	38.0 (37.2–39.0) 6	37.0, 37.3	37.0 (36.1–37.9) 3
GLS	20.7, 21.2	20.2	20.5 (20.2–20.8) 6	20.5 (20.4–20.8) 4
CIL	19.6, 19.5	18.3	18.3 (18.2–18.8) 4	18.6 (18.4–18.7) 4
PB	5.6, 5.5	5.3	5.5 (5.2–5.8) 7	5.4 (5.2–5.6) 4
BB	9.2, 9.0	9.3	9.3 (8.9–9.6) 6	8.9 (8.7–9.1) 4
MB	10.6, 10.6	10.4	10.4 (10.4–10.5) 5	10.3 (10.1–10.4) 4
ZB	12.2, 12.2	—	11.9 (11.6–12.1) 4	11.9 (11.8–12.2) 4
MTL	7.6, 7.8	7.1	7.0 (6.8–7.4) 6	7.4 (7.3–7.5) 4
BAM	8.7, 8.7	8.5	8.5 (8.2–8.9) 7	8.5 (8.4–8.7) 4

[a] MUSM 5500, 5928.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 4211, 4213, 4361, 5927, 32847, 32875.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 73990–73993, 74013; FMNH 89095; MUSM 21222.
[d] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 871, 4217, 5526, 5598.

Platyrrhinus incarum (Thomas, 1912)

Figure 26C

Voucher material (total = 12): Jenaro Herrera (MUSM 4215, 4216, 4218), Nuevo San Juan (MUSM 13241), Quebrada Betilia (MUSA 15165, 15169), Quebrada Blanco (MUSM 21221), Quebrada Esperanza (FMNH 89094), Quebrada Lobo (MUSA 15111), Quebrada Pantaleón (MUSA 15252), Río Blanco (MUSA 15075, 15093); see table 47 for measurements.

Unvouchered observations: During the Sierra del Divisor Rapid Biological Inventory, two individuals of *Platyrrhinus incarum* (identified as *P. helleri*) were captured at Tapiche (Jorge and Velazco, 2006).

Identification: *Platyrrhinus incarum* is a widespread Amazonian species that was originally described as *Vampyrops zarhinus incarum* by Thomas (1912) based on a single specimen from the Department of Pasco, Peru. Sanborn (1955), however, synonymized *incarum* with *P. helleri*, and *incarum* was subsequently treated as a subspecies of *helleri* by many authors (e.g., Koopman, 1978, 1994; Simmons, 2005; Gardner, 2008f). More recently, Velazco and Patterson (2008) restricted *P. helleri* to the Central American populations of the species and applied the name *P. incarum* to the South American populations formerly assigned to *P. helleri*. *Platyrrhinus incarum* is distinguished from other members of the genus by its small size (forearm 35–40 mm); U-shaped notch in the posterior margin of the uropatagium; poorly developed (almost imperceptible) paraoccipital processes; barely perceptible fossa on the squamosal root of the zygomatic arch; two cuspules on the posterior cristid of the second upper premolar; M1 protocone well developed; stylar cuspule present on the lingual face of the paracone of M2; and m2 hypoconid present (Velazco et al., 2010a; López-

TABLE 47

External and Craniodental Measurements (mm) and Weights (g) of *Platyrrhinus incarum*, *P. infuscus*, and *Sphaeronycteris toxophyllum* from the Yavarí-Ucayali Interfluve

	P. incarum		*P. infuscus*		*S. toxophyllum*
	MUSM 13241 ♂	Females[a]	MUSM 15289 ♂	Females[b]	MUSM 32955 ♂
W	9.8	13.0	45.0	48.1 (41.0–56.0) 7	18.0
ToL	55	55, 58	83	87.1 (82–93) 7	63
HF	11	9.7 (8–12) 5	15	15.9 (14–17) 7	11
E	16	17, 17	23	22.1 (22–23) 7	15
F	35.0	37.1 (36.0–39.0) 5	56.0	57.2 (56.0–59.0) 6	39.0
GLS	20.0	21.0	30.1	29.0, 29.0	—
CIL	18.2	19.2	27.6	26.6, 26.8	—
PB	5.3	5.4, 5.5	7.0	6.7, 6.7	—
BB	8.9	9.3, 9.3	12.8	12.5	—
MB	9.8	10.3, 10.6	14.5	14.5, 15.1	—
ZB	11.4	11.9, 12.1	17.9	17.6, 18.0	—
MTL	7.2	7.1, 7.5	11.8	11.3, 11.3	—
BAM	8.5	8.2, 8.7	13.4	12.7	—

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 89094; MUSM 4215–4216, 4218, 21221.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272841–272842, 273047–273048; MUSM 13242, 15259, 15288.

Baucells et al., 2018). Descriptions and measurements of *P. incarum* were provided by Velazco et al. (2010a), Velazco and Lim (2014), and Velazco and Patterson (2019). No subspecies are currently recognized (Velazco et al., 2010a).

Fleck et al. (2002) identified the specimen from Nuevo San Juan as *P.* cf. *helleri*, but Medina et al. (2015) correctly identified their specimens from Quebrada Betilia, Quebrada Lobo, and Quebrada Pantaleón as *P. incarum*. All the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *P. incarum*, with measurements that fall within the previously documented range of intraspecific size variation.

Remarks: Of five specimens of *Platyrrhinus incarum* accompanied by capture information from our region, three were taken in ground-level mistnets and two in elevated nets; of these, two were taken in primary forest, one in secondary vegetation, and two in clearings.

Platyrrhinus infuscus (Peters, 1880)

Voucher material (total = 8): Nuevo San Juan (AMNH 272841, 272842, 273047, 273048; MUSM 13242, 15259, 15288, 15289); see table 47 for measurements.

Unvouchered observations: None.

Identification: *Platyrrhinus infuscus* is known from eastern Colombia, eastern Ecuador, eastern Peru, eastern Bolivia, and western Brazil (Velazco, 2005; Gardner, 2008f). This species is distinguished from other congeners by its large size (forearm >54 mm); buffy to dark-brown dorsal fur; inconspicuous facial and dorsal stripes; short, sparse fur on the dorsal surfaces of the feet; second lower molar with a posterolabial cuspulid; M1 parastyle present; and m1 metaconid well developed (Velazco, 2005; Gardner, 2008f; López-Baucells et al., 2018). Descriptions and measurements of *P. infuscus* have been provided by Cabrera

(1958), Gardner and Carter (1972), Swanepoel and Genoways (1979), Velazco (2005), Velazco and Gardner (2009), and Velazco and Patterson (2019). No subspecies are currently recognized (Gardner, 2008f).

Fleck et al. (2002) correctly identified their specimens from Nuevo San Juan as *Platyrrhinus infuscus*. Their voucher material conforms to previous descriptions of the species, with measurements that fall within the previously documented range of intraspecific size variation.

Remarks: The only specimens of *Platyrrhinus infuscus* accompanied by capture information from our region were collected near Nuevo San Juan, where two were taken in ground-level mistnets in primary forest, one was taken in a ground-level net in secondary vegetation, and five were taken from roosts. We found two roosts of this species, both of them beneath undercut stream banks in primary forest. The first group, encountered on 4 September 1999, consisted of an adult male and three adult females. The second group, encountered on 26 October 1999, also consisted of four individuals, but only a single adult female was collected. Neither roost contained other species of bats.

This species was previously known to roost in caves (Tuttle, 1970; Gardner and Carter, 1972),[12] but, as noted by Gardner (2008f: 337), "the species obviously uses other types of roosts because caves and grottos are scarce in the western Amazon basin," where it is widely distributed. Our observations from Nuevo San Juan suggest that undercut stream banks may be the typical roost of *Platyrrhinus infuscus* in caveless terrain, but Garbino and Tavares (2018) recorded a single instance of this species roosting in a hollow tree.

Sphaeronycteris toxophyllum Peters, 1882

Voucher material (total = 1): Estación Biológica Madre Selva (MUSM 32955); see table 47 for measurements.

[12] Tuttle misidentified his specimens of *Platyrrhinus infuscus* as *Vampyrops vittatus* (see Koopman, 1978).

Unvouchered observations: None.

Identification: *Sphaeronycteris* is a widespread monotypic genus that occurs from eastern Colombia and Venezuela southward into the western Amazon basin of Ecuador, Peru, Brazil, and Bolivia (Simmons, 2005; Angulo et al., 2008; Gardner, 2008g). *Sphaeronycteris toxophyllum* is easily distinguished from other stenodermatines by the presence of the following characteristics: a large, sexually dimorphic fleshy protuberance on the forehead that extends forward above the eyes and noseleaf in males (this structure is present but much smaller in females); a large fold of skin around the neck in males (present but smaller in females); and white spots on the shoulders (Angulo et al., 2008; López-Baucells et al., 2018). Descriptions and measurements of *Sphaeronycteris* have been provided by Husson (1958), Swanepoel and Genoways (1979), Angulo and Díaz (2004), Rodríguez-Posada and Cardenas-Gonzales (2012), and Gallardo et al. (2014). No subspecies are currently recognized (Angulo et al., 2008).

The single voucher we examined (a fluid-preserved specimen) is unambiguously identifiable as *Sphaeronycteris toxophyllum* based on the external characters listed above and external measurements that fall within the range of size variation previously documented for this species.

Remarks: The single individual known from our region was captured in a ground-level mistnet in *várzea* (seasonally inundated riparian forest) about 50 m from the Río Orosa (Angulo and Díaz, 2004).

Genus *Sturnira* Gray, 1842

The genus *Sturnira* is widespread in the Neotropics and includes 24 currently recognized species, up to five of which are known to occur in sympatry at some localities (Velazco and Patterson, 2013, 2014, 2019; Simmons and Cirranello, 2020). Species of *Sturnira* can be distinguished from members of other stenodermatine genera by the presence of shoulder glands (epaulettes) that stain the fur, especially in adult males; absence of

TABLE 48

External and Craniodental Measurements (mm) and Weights (g) of *Sturnira giannae* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	22, 23	20.0 (18–24) 3
ToL	66.3 (65–69) 3	62.3 (60–65) 3
HF	12.7 (12–14) 3	12.0 (11–13) 3
E	17.0 (17–17) 3	16.7 (16–17) 3
F	44.3 (44.0–45.0) 3	44.8 (44.6–45.0) 3
GLS	22.6 (22.3–22.9) 3	22.3 (22.1–22.5) 3
CIL	21.1 (20.7–21.5) 3	21.0 (20.6–21.3) 3
PB	(5.8) 3	5.7 (5.5–6.0) 3
BB	10.5 (10.2–10.9) 3	10.1 (9.8–10.5) 3
MB	12.4 (12.2–12.5) 3	12.2 (11.5–12.9) 3
ZB	13.9, 14.2	13.2
MTL	6.8 (6.5–7.0) 3	6.9 (6.8–7.1) 3
BAM	8.2 (8.2–8.3) 3	8.3 (8.2–8.3) 3

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 87058; MUSM 5925, 21266.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of MUSM 5922, 5924, 13260.

an external tail; absence of a calcar; a narrow uropatagium that often is hidden under the dense fur covering the membrane and legs; last upper premolar and upper molars with cusps shifted to the labial and lingual margins, where they border a broad, longitudinal groove that is continuous from tooth to tooth; and lower molar cusps arranged in a similar manner, except that the groove is interrupted by the paraconid anteriorly (Gardner, 2008h). Gardner (2008h) provided a key to the species based on external and craniodental characters, but subsequent descriptions of new species limit its usefulness. The three species expected to occur in the Yavarí-Ucayali interfluve were all recorded during our study.

Sturnira giannae Velazco and Patterson, 2019

Voucher material (total = 7): Isla Muyuy (MUSM 21266), Jenaro Herrera (MUSM 5922, 5924, 5925), Nuevo San Juan (MUSM 13260), Quebrada Pantaleón (MUSA 15262), Santa Cecilia (FMNH 87058); see table 48 for measurements.

Unvouchered observations: None.

Identification: *Sturnira giannae* is a widespread Amazonian species that also occurs on the eastern slopes of the Andes (Velazco and Patterson, 2019). *Sturnira giannae* is distinguished from other congeners by the following combination of characteristics: dorsal fur short and bicolored; ventral fur short and monocolored; shoulder glands (epaulettes) present; trailing edge of the uropatagium covered with short hairs; anterior process of the glenoid fossa well-developed; inner upper incisors bicuspidate and slender; inner and outer lower incisors tricuspidate and subequal in height; and lower-molar metaconids and entoconids well defined and separated by a deep notch (Velazco and Patterson, 2019). A description and measurements of *S. giannae* were provided by Velazco and Patterson (2019). No subspecies are currently recognized (Velazco and Patterson, 2019).

Specimens from Jenaro Herrera, Nuevo San Juan and Quebrada Pantaleón were previously identified by Ascorra et al. (1993), Fleck et al.

TABLE 49

External and Craniodental Measurements (mm) and Weights (g) of *Sturnira magna* and *S. tildae* from the Yavarí-Ucayali Interfluve

	S. magna		*S. tildae*	
	Males[a]	Females[b]	MUSM 5923 ♂	Females[c]
W	36, 45	40, 44	21	25, 35
ToL	90.7 (87–95) 3	88.0 (85–91) 5	74	72.3 (69–76) 3
HF	19.7 (18–21) 3	18.8 (17–20) 5	11	13.3 (13–14) 3
E	21.7 (21–22) 3	21.8 (21–22) 5	19	19.7 (19–20) 3
F	58.0 (57.0–59.0) 3	58.6 (57.0–61.0) 5	47.8	49.0 (47.1–50.0) 3
GLS	28.1	27.3 (26.4–28.2) 4	22.6	24.1, 22.5
CIL	26.3	25.4, 25.6	21.5	21.3, 22.1
PB	7.4	7.1 (7.0–7.3) 4	6.4	5.8, 6.6
BB	12.1	12.2 (11.9–12.4) 4	10.4	10.7, 11.0
MB	15.3	14.6 (14.3–15.2) 4	12.6	12.1, 12.7
ZB	17.3	—	—	14.0, 14.1
MTL	7.7	7.6 (7.3–7.7) 4	6.7	6.8, 7.1
BAM	9.4	9.1 (8.9–9.3) 4	8.4	8.1, 8.3

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272787; FMNH 87059; MUSM 13261.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272815; FMNH 87060–87062; MUSM 5496.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of CEBIOMAS 109; MUSM 5921, 5926.

(2002), and Medina et al. (2015), respectively as *Sturnira lilium*. Voucher material from the Yavarí-Ucayali interfluve conforms to Velazco and Patterson's (2019) description of *S. giannae* in all qualitative and quantitative respects.

Remarks: The only specimen of *Sturnira giannae* accompanied by capture information from our region was taken in a ground-level mistnet in a swampy mineral lick (*collpa*) near Nuevo San Juan.

Sturnira magna de la Torre, 1966

Figure 27A

Voucher material (total = 13): Jenaro Herrera (MUSM 5496), Nuevo San Juan (AMNH 272787, 272815; MUSM 13261), Quebrada Betilia (MUSA 15170, 15197), Quebrada Lobo (MUSA 15123), Quebrada Sábalo (MUSA 15212, 15239), Santa Cecilia (FMNH 87059–87062); see table 49 for measurements.

Unvouchered observations: One individual of *Sturnira magna* was captured at the Quebrada Limera locality during the Yavarí Rapid Biological Inventory (Escobedo, 2003).

Identification: *Sturnira magna* can be distinguished from other congeners by its large size (forearm >51 mm, greatest length of skull >27 mm); U-shaped posterior border of the hard palate; first upper incisors blunt and in contact; and lower-molar metaconids and entoconids poorly defined, usually forming a continuous, sloping lingual ridge (Gardner, 2008h; López-Baucells et al., 2018). Descriptions and measurements of *S. magna* were provided by de la Torre (1966), Peterson and Tamsitt (1968), Gardner (1976), Swanepoel and Genoways (1979), and Tamsitt and Häuser (1985). No subspecies are currently recognized (Gardner, 2008h).

A
B

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their material from Jenaro Herrera, Nuevo San Juan, Quebrada Betilia, Quebrada Lobo, and Quebrada Sábalo. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Sturnira magna*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: The only specimens of *Sturnira magna* accompanied by capture data from our region were taken in ground-level mistnets near Nuevo San Juan, one in upland primary forest and two others in a swampy mineral lick (*collpa*).

Sturnira tildae de la Torre, 1959

Voucher material (total = 5): Jenaro Herrera (CEBIOMAS 109; MUSM 5921, 5923, 5926), Río Blanco (MUSA 15080); see table 49 for measurements.

Unvouchered observations: None.

Identification: *Sturnira tildae* can be distinguished from other species of *Sturnira* by its medium size (forearm 43–51 mm, greatest length of skull 24–26 mm); tricolored dorsal fur; shoulder glands (epaulettes) present and well defined; metacarpal III shorter than metacarpal V; inner upper incisors broad and weakly bicuspid, with lobes of equal size; lower-molar metaconids and entoconids well defined and separated by a notch; and paraconulids absent on m1 and m2 (Gardner, 2008h; López-Baucells et al., 2018). Descriptions and measurements of *S. tildae* were provided by de la Torre (1959), Goodwin and Greenhall (1961), Hill (1964), Marinkelle and Cadena (1971), Husson (1978), Genoways and Williams (1979), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Ochoa-G. et al. (1993), Simmons and Voss (1998), Lim et al. (2005), Jarrín-V and Kunz (2011), and Velazco and Patterson (2019). No subspecies are currently recognized (Gardner, 2008h).

Ascorra et al. (1993) and Medina et al. (2015) correctly identified their specimens from Jenaro Herrera and Río Blanco, respectively. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Sturnira tildae*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Of seven recorded captures of *Sturnira tildae* accompanied by ecological information from our region, four were taken in ground-level mistnets and three in elevated nets. Of these mistnet captures, four were in primary forest, two were in secondary vegetation, and one was on a river beach.

Genus *Uroderma* Peters, 1865

The genus *Uroderma* currently includes five species (Mantilla-Meluk, 2014; Cuadrado-Ríos and Mantilla-Meluk, 2016; Simmons and Cirranello, 2020). *Uroderma* is distinguished from other genera by the following combination of characteristics: presence of white facial stripes and a white middorsal stripe; lack of a fringe of hairs along the trailing edge of a deeply notched uropatagium; relatively large, evenly bifid upper inner incisors; and presence of three upper and lower molars (Gardner, 2008i). The two species expected to occur in the Yavarí-Ucayali interfluve were both recorded during our study.

Uroderma bilobatum Peters, 1865

Voucher material (total = 30): Boca Río Yaquerana (FMNH 89082), Isla Padre (MUSM 4212, 4365), Estación Biológica Madre Selva (MUSM 33146), Jenaro Herrera (AMNH 278506; MUSM 872, 4220), Nuevo San Juan (MUSM 13281), Quebrada Betilia (MUSA 15192, 15202), Quebrada Esperanza (FMNH 89084, 89086, 89130, 89131, 89136), Quebrada Lobo (MUSA 15114), Quebrada Vainilla (LSUMZ 28433), Río Blanco (MUSA 15085, 15091, 15103), Santa

FIG. 27. Photographs of **A,** an adult *Sturnira magna* captured at Quebrada Blanco; and **B,** an adult *Uroderma magnirostrum* captured at El Chino Village. Photographs by Marco Tschapka (A) and Brock Fenton (B).

TABLE 50

External and Craniodental Measurements (mm) and Weights (g) of *Uroderma bilobatum* and *U. magnirostrum* from the Yavarí-Ucayali Interfluve

	U. bilobatum		*U. magnirostrum*	
	Males[a]	Females[b]	MUSM 4362 ♂	Females[c]
W	18, 22	23.7 (18–34) 3	—	–, –
ToL	62.7 (60–66) 7	66.3 (65–69) 8	—	–, 65
HF	10.7 (8–13) 11	10.9 (8–13) 13	9	11, 9
E	18.0 (16–20) 7	17.6 (17–18) 8	—	–, 17
F	42.2 (40.0–43.4) 11	42.1 (37.0–45.0) 13	41.5	43.6, 44.8
GLS	23.7 (22.4–24.0) 7	23.3 (22.3–23.9) 7	—	–, 23.2
CIL	21.5 (20.0–22.0) 7	21.3 (20.7–21.6) 7	—	–, 21.6
PB	5.5 (5.2–5.8) 7	5.5 (5.3–5.8) 7	—	–, 6.2
BB	9.9 (9.6–10.3) 7	9.7 (9.4–10.1) 7	—	–, 10.0
MB	11.2 (10.8–11.4) 7	11.1 (10.6–11.7) 7	—	–, 11.5
ZB	13.1 (12.4–13.6) 5	13.2 (12.8–13.7) 4	—	–, 13.0
MTL	8.3 (7.8–8.7) 7	8.1 (7.9–8.4) 7	—	–, 7.9
BAM	9.2 (8.6–9.5) 7	9.3 (8.9–9.6) 7	—	–, 9.1

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 278506; FMNH 87040, 87042, 87084, 89082, 89086, 89128; LSUMZ 28433; MUSM 4212, 4220, 4365.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 87038–87039, 87041, 87043, 89084, 89127, 89129–89131, 89136; MUSM 872, 13281, 33146.
[c] MUSM 4364, 5595.

Cecilia (FMNH 87038–87043, 87084, 89127–89129); see table 50 for measurements.

Unvouchered observations: One individual of *Uroderma bilobatum* was captured at Tapiche during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006). Additionally, an unspecified number of individuals of *U. bilobatum* were captured at Quebrada Pobreza during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015), one individual was captured at the Quebrada Curacinha locality during the Yavarí Rapid Biological Inventory (Escobedo, 2003), and we captured one individual at Tahuayo Farm on 19 February 2019.

Identification: The taxonomy and systematics of the *Uroderma bilobatum* species complex was recently reviewed by Mantilla-Meluk (2014) and Cuadrado-Ríos and Mantilla-Meluk (2016), who recognized four species: *U. bilobatum*; *U. convexum* and *U. davisi*, both formerly treated as subspecies of *U. bilobatum*; and a newly described species, *U. bakeri*. As a result, *U. bilobatum* (sensu stricto) is now restricted to lowland South American populations east of the Andes. *Uroderma bilobatum* can be distinguished from other congeneric species by the following combination of characteristics: brownish dorsal and ventral pelage; prominent facial stripes; dorsum of uropatagium nearly naked; rostrum not elevated and with a dorsal concavity; interorbital constriction not swollen; and junction of nasals and maxillae forms an obtuse angle in lateral view (Mantilla-Meluk, 2014). Descriptions and measurements of *U. bilobatum* were provided by Goodwin and Greenhall (1961), Husson (1962, 1978), Ceballos-Bendezú (1968), Davis (1968), Carter and Dolan (1978), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Lim et al. (2005), Mantilla-Meluk (2014), and Velazco and

Patterson (2019). Three subspecies are currently recognized: *U. b. bilobatum* (Amazonian lowlands and the Atlantic Forest); *U. b. thomasi* (middle elevations on the eastern slopes of the Andes in Ecuador, Peru, and Bolivia); and *U. b. trinitatum* (Trinidad) (Mantilla-Meluk, 2014; Cuadrado-Ríos and Mantilla-Meluk, 2016).

Ceballos-Bendezú (1968), Fleck et al. (2002), and Medina et al. (2015) correctly identified their material from Quebrada Esperanza, Nuevo San Juan, Quebrada Betilia, Quebrada Lobo, and Río Blanco. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Uroderma bilobatum bilobatum*, with measurements that fall within the range of size variation previously documented for the nominotypical subspecies.

Remarks: Of nine captures of *Uroderma bilobatum* accompanied by ecological information from our region, six were made in ground-level mistnets and three in elevated nets. Of these mistnet captures, three were in primary forest, two were in secondary vegetation, three were in clearings, and one was in a swampy mineral lick (*collpa*).

Uroderma magnirostrum Davis, 1968

Figure 27B

Voucher material (total = 3): Isla Padre (MUSM 4362, 4364), Jenaro Herrera (MUSM 5595); see table 50 for measurements.

Unvouchered observations: One individual each of *Uroderma magnirostrum* were captured at Quebrada Curacinha and Quebrada Limera during the Yavarí Rapid Biological Inventory (Escobedo, 2003). Additionally, we captured one individual at El Chino Village on 18 February 2019.

Identification: This is a widespread but apparently uncommon species distributed from Mexico to eastern Brazil (Gardner, 2008i; Reid, 2009). *Uroderma magnirostrum* is easily distinguished from other congeneric species by its paler dorsal and ventral pelage; less prominent facial stripes; dorsal surface of uropatagium hairy beyond the level of the knees; rostrum deep; dorsal profile from crown to tip of snout nearly a straight line; and mesethmoid greatly expanded, broad, and shield shaped in frontal view (Davis, 1968; Gardner, 2008i; López-Baucells et al., 2018). Descriptions and measurements of *U. magnirostrum* were provided by Davis (1968), Swanepoel and Genoways (1979), Willig (1983), and Nogueira et al. (2003). No subspecies are currently recognized (Gardner, 2008i).

Ascorra et al. (1993) correctly identified their specimen from Jenaro Herrera. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Uroderma magnirostrum*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Escobedo (2003) reported capturing *Uroderma magnirostrum* over a stream at Quebrada Limera, and the individual captured at El Chino Village was taken in a ground-level mistnet in a clearing.

Vampyressa thyone Thomas, 1909

Figure 28A

Voucher material (total = 36): Boca Río Yaquerana (FMNH 89053–89056, 89139, 89140), Estación Biológica Madre Selva (MUSM 33327), Jenaro Herrera (AMNH 278511; CEBIOMAS 113, 114; MUSM 4223), Quebrada Betilia (MUSA 15189–15191), Quebrada Blanco (MUSM 21185), Quebrada Esperanza (FMNH 89059–89067, 89141, 89143, 89145), Quebrada Lobo (MUSA 15112, 15126, 15129, 15137, 15138), Quebrada Sábalo (MUSA 15214, 15215), Quebrada Vainilla (LSUMZ 28439), Santa Cecilia (FMNH 87103); see table 51 for measurements.

Unvouchered observations: *Vampyressa thyone* (identified as *V. pusilla*; see below) was captured at Divisor (one individual) and Tapiche (one individual) during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006).

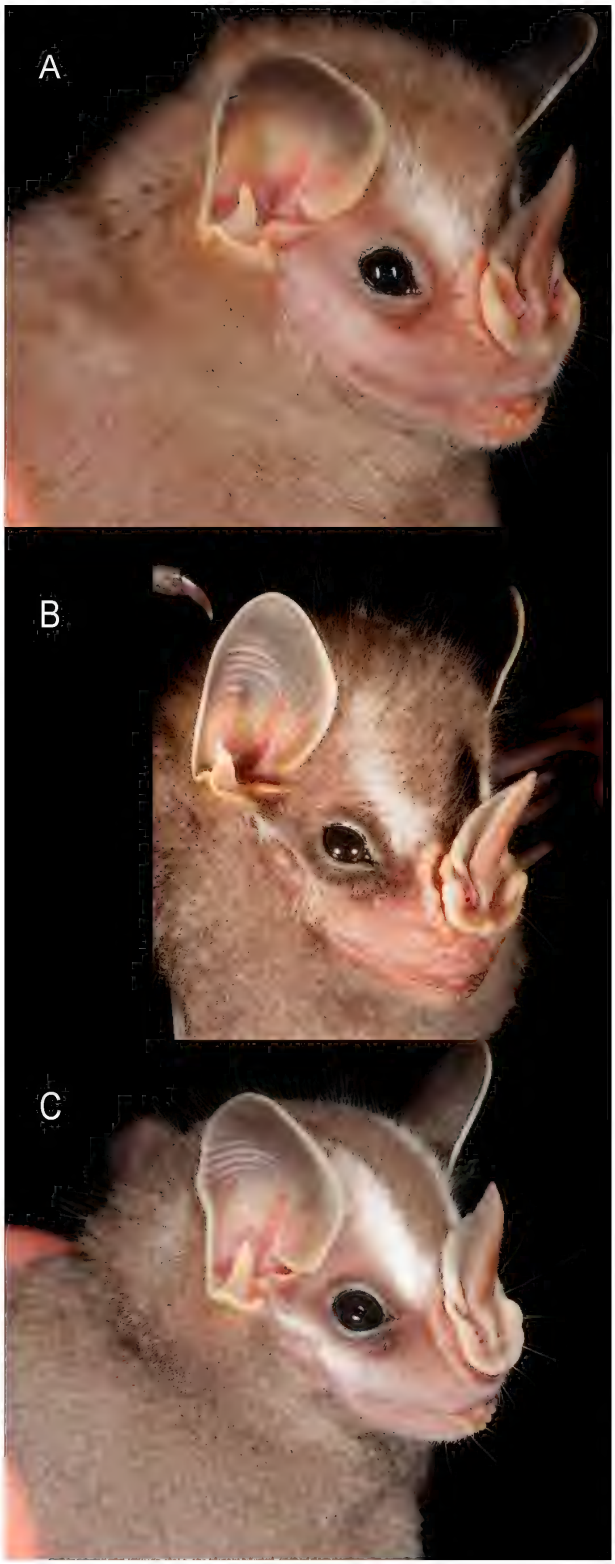


FIG. 28. Photographs of **A,** an adult *Vampyressa thyone* captured at Jenaro Herrera; **B,** an adult *Vampyriscus bidens* captured at El Chino Village; and **C,** an adult *Vampyriscus brocki* captured at Jenaro Herrera. Photographs by Marco Tschapka (A, C) and Brock Fenton (B).

TABLE 51

External and Craniodental Measurements (mm) and Weights (g) of *Vampyressa thyone* and *Vampyrodes caraccioli* from the Yavarí-Ucayali Interfluve

	Vampyressa thyone		*Vampyrodes caraccioli*
	Males[a]	Females[b]	MUSA 15124 ♂
W	6.5 (6–7) 4	7.5, 9.5	29.5
ToL	43.9 (41–46) 9	46.4 (44–50) 11	78
HF	8.6 (6–10) 9	8.9 (7–10) 17	16
E	14.1 (12–15) 9	14.0 (13–16) 11	19
F	30.4 (29.0–32.0) 9	30.6 (29.5–32.0) 17	52.4
GLS	17.5 (16.9–18.5) 9	17.7 (17.3–18.2) 10	—
CIL	16.1 (15.5–17.0) 8	16.3 (16.0–16.8) 10	—
PB	4.6 (4.0–5.0) 9	4.6 (4.4–4.8) 11	—
BB	8.1 (7.6–8.8) 9	8.3 (8.1–8.6) 12	—
MB	8.8 (8.4–9.2) 9	8.9 (8.7–9.2) 12	—
ZB	10.2 (9.6–10.7) 7	10.4 (10.3–10.6) 9	—
MTL	5.6 (5.3–6.0) 9	5.6 (5.4–5.9) 12	—
BAM	7.2 (6.7–7.8) 9	7.2 (6.9–7.6) 10	—

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of CEBIOMAS 113–114; FMNH 89053–89054, 89064–89066; LSUMZ 28439; MUSM 21185.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 278511; FMNH 87103, 89055–89056, 89059–89063, 89067, 89139–89141, 89143, 89145; MUSM 4223, 33327.

Identification: The genus *Vampyressa* includes six currently recognized species (Simmons and Cirranello, 2020; Morales-Martínez et al., 2021), only one of which is known from the Yavarí-Ucayali interfluve. *Vampyressa thyone* (formerly often confused with *V. pusilla*, a southeastern Brazilian and Paraguayan species; Lim et al., 2003) can be distinguished from other stenodermatines by the following characteristics: small size (forearm <34 mm, greatest length of skull <19 mm); presence of inconspicuous facial stripes and lack of a middorsal stripe; uropatagium narrow and sparsely haired; rostrum shorter than braincase; hard palate extending well behind the molars; long upper inner incisors separated basally but converging at their bifid tips; first upper premolar smaller than the second; and first lower premolar caniniform and smaller than the second (Arroyo-Cabrales, 2008b). Descriptions and measurements of *Vampyressa thyone* have been provided by Goodwin (1963), Ceballos-Bendezú (1968), Lim et al. (2003), Tavares et al. (2014), and Velazco and Patterson (2019). No subspecies are currently recognized (Arroyo-Cabrales, 2008b), but *venilla* Thomas, 1924 (a synonym), was formerly used as such (e.g., by Ceballos-Bendezú (1968).

Ceballos-Bendezú (1968) and Medina et al. (2015) correctly identified their specimens from Boca Río Yaquerana, Quebrada Esperanza, Quebrada Betilia, Quebrada Lobo, and Quebrada Sábalo. The voucher material that we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Vampyressa thyone*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Only seven recorded captures of *Vampyressa thyone* are accompanied by ecological data from our region, including five that were made in ground-level mistnets and two in elevated nets. Of these mistnet captures, two were

made in primary forest, another two in secondary vegetation, and three in clearings.

Genus *Vampyriscus* Thomas, 1900

Previously ranked as a subgenus of *Vampyressa* (e.g., by Simmons, 2005), *Vampyriscus* is now considered a distinct genus that includes three currently recognized species (Arroyo-Cabrales, 2008c; Simmons and Cirranello, 2020). Species of *Vampyriscus* can be distinguished from members of other stenodermatine genera by the following combination of characteristics: noseleaf with a well-defined median rib; uropatagium relatively narrow and sparsely haired; rostrum shorter than braincase; first upper incisors long, separated basally, and with pointed or weakly bifid tips; basisphenoid pits shallow; lower first premolar not caniniform; and only two upper molars present (Arroyo-Cabrales, 2008c). We recorded both species of *Vampyriscus* that are expected to occur in the Yavarí-Ucayali interfluve.

Vampyriscus bidens (Dobson, 1878)

Figure 28B

Voucher material (total = 3): Quebrada Blanco (MUSM 21320), Santa Cecilia (FMNH 87075, 87076); see table 52 for measurements.

Unvouchered observations: An unspecified number of individuals of *Vampyriscus bidens* were captured at Wiswincho during the Tapiche-Blanco Rapid Biological Inventory (Escobedo-Torres, 2015). Additionally, we captured three individuals at El Chino Village, two on 16 February and another on 18 February 2019.

Identification: *Vampyriscus bidens* can be easily distinguished from other congeneric species by the presence of a well-defined pale middorsal stripe, presence of only one pair of lower incisors, and a minute m3 (Arroyo-Cabrales, 2008c; López-Baucells et al., 2018). Descriptions and measurements of *Vampyriscus bidens* were provided by Davis (1975), Genoways and Williams (1979), Swanepoel and Genoways (1979), Brosset and Charles-Dominique (1990), Lee et al. (2001), and Shapley et al. (2005). No subspecies are currently recognized (Arroyo-Cabrales, 2008c).

The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Vampyriscus bidens*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: The only specimens of *Vampyriscus bidens* accompanied by capture data from our region were taken in clearings and gardens at El Chino; of these, two were taken in a harp trap and one was taken in a ground-level mistnet.

Vampyriscus brocki (Peterson, 1968)

Figure 28C

Voucher material (total = 17): Jenaro Herrera (MUSM 5942, 6979), Quebrada Betilia (MUSA 15168), Quebrada Esperanza (FMNH 89142), Quebrada Lobo (MUSA 15130), Quebrada Vainilla (LSUMZ 28438), Santa Cecilia (FMNH 87097–87102, 87104–87107, 89137); see table 52 for measurements.

Unvouchered observations: One individual of *Vampyriscus brocki* was captured at Quebrada Limera during the Yavarí Rapid Biological Inventory (Escobedo, 2003). Additionally, we captured one individual at El Chino Village on 18 February 2019. *Vampyriscus brocki* was also identified using acoustic methods during the CEBIO bat course at Jenaro Herrera.

Identification: *Vampyriscus brocki* can be distinguished from other congeneric species by its relatively small size (forearm <35 mm), middorsal stripe faint or absent, presence of two pairs of lower incisors, and absence of m3 (Simmons and Voss, 1998; Arroyo-Cabrales, 2008c; López-Baucells et al., 2018). Descriptions and measurements of *Vampyriscus brocki* have been provided by Swanepoel and Genoways (1979), Simmons and Voss (1998), Lim et al. (2005), and Ruelas and Pacheco (2015). No subspecies are currently recognized (Arroyo-Cabrales, 2008c).

TABLE 52

External and Craniodental Measurements (mm) and Weights (g) of *Vampyriscus bidens* and *V. brocki* from the Yavarí-Ucayali Interfluve

	V. bidens		*V. brocki*	
	Males[a]	FMNH 87075 ♀	Males[b]	Females[c]
W	–, 12	—	7.9	8.0 (8–8) 2
ToL	56, 56	54	46.8 (42.5–49.0) 3	48.4 (45–51) 10
HF	11, 8	11	9.5 (9–10) 3	9.3 (8–11) 12
E	16, 16	16	14.3 (14–15) 3	15.1 (14–16) 10
F	35.0, 35.5	35.5	32.3 (31.0–33.0) 3	32.7 (31.7–34.5) 12
GLS	–, 18.9	20.0	17.8, 18.5	18.1 (17.8–18.4) 7
CIL	–, 17.3	18.0	15.7, 16.5	16.3 (15.9–16.6) 6
PB	4.8, 5.4	5.4	4.9 (4.5–5.2) 3	5.0 (4.9–5.1) 8
BB	–, 9.1	9.2	8.4, 8.7	8.4 (8.3–8.5) 9
MB	–, 10.1	10.5	9.3, 9.5	9.4 (9.0–9.7) 9
ZB	–, 12.1	—	10.8, 11.0	10.8 (10.4–11.1) 6
MTL	6.5, 6.3	6.7	5.8 (5.7–5.9) 3	5.8 (5.3–6.3) 8
BAM	7.7, 8.3	8.4	7.6, 7.7	7.7 (7.4–8.0) 5

[a] FMNH 87076; MUSM 21320.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 87098, 87102; LSUMZ 28438.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of FMNH 87097, 87099–87101, 87104–87107, 89137, 89142; MUSM 5942, 6979.

Ascorra et al. (1993) and Medina et al. (2015) correctly identified their material from Jenaro Herrera, Quebrada Betilia, and Quebrada Lobo as *Vampyriscus* (or *Vampyressa*) *brocki*.

Remarks: Of eight recorded captures of *Vampyriscus brocki* accompanied by ecological data from our region, four were taken in ground-level mistnets and four in elevated nets; four of these mistnet captures were in primary forest and four were in clearings. Additionally, Escobedo (2003) reported capturing this species in seasonally flooded forest.

Vampyrodes caraccioli (Thomas, 1889)

Figure 29

Voucher material (total = 1): Quebrada Lobo (MUSA 15124); see table 51 for measurements.

Unvouchered observations: One individual of *Vampyrodes caraccioli* was captured at Tapiche during the Sierra del Divisor Rapid Biological Inventory (Jorge and Velazco, 2006), and we captured a single individual at El Chino Village on 18 February 2019 (fig. 29).

Identification: Before the revision by Velazco and Simmons (2011), *Vampyrodes caraccioli* was the sole member of the genus and was thought to range from Mexico to eastern Brazil. Two subspecies (*V. c. caraccioli* and *V. c. major*) were traditionally recognized (Koopman, 1994; Gardner, 2008j). After morphological, morphometric, and molecular analyses, Velazco and Simmons (2011) concluded that the two subspecies represented distinct species, of which only *V. caraccioli* sensu stricto is known to occur in South America east of the Andes.

Vampyrodes caraccioli can be distinguished from other cis-Andean stenodermatines by the

FIG. 29. Photograph of an adult male *Vampyrodes caraccioli* captured at El Chino Village. Photograph by Brock Fenton.

following characteristics: prominent white dorsal stripe and conspicuous white facial stripes, bicolored dorsal fur, tricolored ventral fur, presence of a fringe of hairs on the edge of the uropatagium, lingual cingula absent at the bases of the metacones of the upper molars, lack of M3, the presence of two cuspules on the posterior cristid of the second upper premolar, and lingual cingulid absent on the first lower molar (Gardner, 2008j; Velazco and Simmons, 2011). Descriptions and measurements of *V. caraccioli* were provided by Husson (1954), Swanepoel and Genoways (1979), Lim et al. (2005), Velazco et al. (2010b), Velazco and Simmons (2011), Carvalho et al. (2014), Lopes et al. (2016), and Althoff et al. (2017). No subspecies are currently recognized (Velazco and Simmons, 2011).

Medina et al. (2015) identified the specimen from Quebrada Lobo as *Vampyrodes caraccioli* based only on external characters because the skull had not been removed from the body. Nevertheless, the provenance of the specimen in addition to the presence of a few characteristics observable in fluid specimens (presence of a fringe of hairs on the edge of the uropatagium, lack of M3, and the presence of two cuspules on the posterior cristid of the second upper premolar) confirms the identity of the specimens as *V. caraccioli*.

TABLE 53

External and Craniodental Measurements (mm) and Weights (g) of *Furipterus horrens* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	3.6 (3.3–3.9) 13	5.1, 4.2
ToL	61.4 (53–66) 13	66, 66
LT	22.6 (14–28) 13	28, 27
HF	8.5 (7–10) 13	8, 8
E	9.6 (9–10) 13	10, 10
F	35.2 (33.0–38.0) 9	38.0, 37.0
GLS	11.7 (11.6–11.9) 5	11.4, 11.8
CIL	11.0 (10.8–11.2) 5	10.9, 11.0
BB	5.8 (5.6–6.0) 5	5.7, 5.8
ZB	7.4 (7.2–7.6) 3	7.2, 7.5
MTL	4.7 (4.7–4.8) 5	4.7, 4.7
BAM	4.8 (4.7–5.0) 5	4.8, 4.9
BAC	2.9 (2.8–3.1) 5	2.7, 3.0

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74108, 272837, 272864, 273071, 273099, 273107; LSUMZ 28445–28446; MUSM 13202–13203, 15190–15193.
[b] AMNH 273068, 273181.

Remarks: The individual from El Chino Village was captured in a ground-level mistnet.

Family Furipteridae Gray, 1866

The Neotropical family Furipteridae includes two monotypic genera, *Amorphochilus* and *Furipterus* (Simmons, 2005; Gardner, 2008k; Simmons and Cirranello, 2020). These taxa can be distinguished from other Neotropical bats by their relatively small size (forearm <39 mm); a blunt muzzle with anteriorly directed nostrils; a tail that is sheathed in the uropatagium, but does not reach the posterior margin of that membrane; a short, triangular tragus; a highly reduced thumb that is enclosed in the wing membrane; a globose braincase that is elevated well above the rostrum; a dentary with a well-developed mental spur; and short upper and lower canines that are about as tall as the crown of the tallest premolar (Simmons and Voss, 1998; Gardner, 2008k). We recorded the only furipterid species expected to occur in the Yavarí-Ucayali Interfluve.

Furipterus horrens (Cuvier, 1828)

Figure 30

Voucher material (total = 17): Nuevo San Juan (AMNH 272837, 272864, 273068, 273071, 273099, 273107, 273181; MUSM 13202, 13203, 15190–15194), Orosa (AMNH 74108), Quebrada Vainilla (LSUMZ 28445, 28446); see table 53 for measurements.

Unvouchered observations: One individual of *Furipterus horrens* was captured but escaped at Jenaro Herrera (Ascorra et al., 1993). During the CEBIO bat course in Jenaro Herrera, one individual was observed roosting in a cavity beneath a fallen tree on 17 January 2012 (fig. 30).

Identification: *Furipterus horrens* is a widespread species that occurs from Nicaragua southward throughout most of humid-tropical South America (Gardner, 2008k; Reid, 2009; Medina-Fitoria et al., 2015). It is easily distinguished from *Amorphochilus schnablii*, the only other species of furipterid, by its rounded, funnel-shaped ears; well-furred muzzle; lack of fleshy

FIG. 30. Photograph of an adult *Furipterus horrens* roosting in a cavity formed by a fallen tree at Jenaro Herrera. Photograph by Alexander Pari.

structures under the chin; a short palate that does not extend much beyond the last molar; and a mesopterygoid fossa that is longer than wide (Gardner, 2008k). Descriptions and measurements of *Furipterus* have been provided by Husson (1962, 1978), Uieda et al. (1980), Willig (1983), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Gardner (2008k), Reid (2009), Duda et al. (2012), Novaes et al. (2012), and Leal et al. (2014). No subspecies are currently recognized (Gardner, 2008k).

Fleck et al. (2002) correctly identified their specimens from Nuevo San Juan. Voucher material from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Furipterus horrens*, with measurements that fall within the range of size variation previously documented for the species. In life the Nuevo San Juan specimens had reddish muzzles and chins, but this coloration has faded in preservative. *Furipterus horrens* is reported to show sexual dimorphism in some populations, with females having larger body size than males (e.g., Uieda et al., 1980; Simmons and Voss, 1998), but no size dimorphism was observed in our voucher specimens.

Remarks: All the specimens of *Furipterus horrens* from our region were taken from roosts, of which we found 10 near Nuevo San Juan (table 54). Most roosting groups of this species were encountered at ground level, but one individual was said (by the Matses hunter who collected it) to have been found roosting high up inside a large hollow tree; possibly it had been

TABLE 54

Roosting Groups of *Furipterus horrens* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
30 Jun 1998	undercut earth bank	2	no	1 ad. male
5 Jul 1998	under fallen tree	4–5	no	2 ad. males
8 Sep 1999	inside hollow log	2	yes	1 ad. male, 1 ad. female
9 Sep 1999	under fallen tree	1	yes	1 ad. male
17 Sep 1999	inside hollow log	1	yes	1 ad. male
17 Sep 1999	cavity in standing tree	1	yes	1 ad. male
22 Sep 1999	crack in fallen tree	1	yes	1 ad. male
28 Sep 1999	inside hollow log	2	yes	2 ad. males
6 Oct 1999	cavity in standing tree	3	no	2 ad. males
26 Oct 1999	inside hollow log	2	yes	1 ad. female, 1 juv. (sex unknown)

frightened upward from some lower perch. Most roosts were in primary upland forest—in well-drained valley bottoms, hillcrests, and hillsides—but two were in seasonally flooded forest. *Furipterus horrens* was not found roosting with any other species of bats.

Of the 23 known natural roosts of this species (LaVal, 1977; Simmons and Voss, 1998; Rengifo et al., 2013; this study), almost 90% were cavities inside or on the underside of fallen trees, which would appear to be the preferred diurnal refugia of this common but seldom-collected bat in caveless regions.

Family Thyropteridae Miller, 1907

The Neotropical family Thyropteridae includes a single genus with five species characterized by small size; the presence of a fleshy circular disk on the sole of each foot; a fleshy oval or circular disk attached by a short pedicle to the base of each thumb; and fusion of the soft tissues of digits III and IV of each foot to form a single conjoined structure (Simmons and Voss, 1998; Velazco et al., 2014). Velazco et al. (2014) provided a key to the species, of which four are represented in the voucher material we examined from the Yavarí-Ucayali interfluve.

Thyroptera discifera (Lichtenstein and Peters, 1854)

Voucher material (total = 1): Jenaro Herrera (MUSM 5546); see table 55 for measurements.

Unvouchered observations: None.

Identification: *Thyroptera discifera* is distinguished from other congeners by the following combination of characteristics: unicolored yellowish-brown ventral pelage; proximal portion of the forearm well furred; adhesive disk at base of thumb circular; calcar with just one posterolaterally projecting lappet; foramen ovale small; outer upper incisor with mesial cusp larger than distal cusp; both cusps on the outer upper incisor obliquely arranged relative to the long axis of the toothrow; first upper premolar elongated in occlusal view; and outer lower incisor with two small accessory cusps (mesostyle and distostyle) (Velazco et al., 2014; López-Baucells et al., 2018). Descriptions and measurements of *T. discifera* were provided by Wilson (1978), Pine (1993), Solari et al. (2004), Bezerra et al. (2005), Gregorin et al. (2006), and Velazco et al. (2014). Two subspecies are currently recognized, of which only the nominotypical form occurs in South America (Wilson, 2008a).

TABLE 55

External and Craniodental Measurements (mm) and Weights (g) of *Thyroptera discifera* and *T. wynneae* from the Yavarí-Ucayali Interfluve

	T. discifera	*T. wynneae*
	MUSM 5546 ♂	AMNH 278486 ♂
W	--	3.5
ToL	69	68
LT	29	26
HF	5	4
E	10	11
F	33.4	33.0
GLS	14.4	13.2
ZB	7.4	6.8
MTL	5.6	5.3
BAM	5.0	4.8

Ascorra et al. (1993), Solari et al. (2004), and Velazco et al. (2014) correctly identified the specimen from Jenaro Herrera, which conforms to previous descriptions and measurements of *Thyroptera discifera*.

Remarks: No ecological information is available about *Thyroptera discifera* in our region.

Thyroptera lavali Pine, 1993

Voucher material (total = 5): Jenaro Herrera (MUSM 5944), Quebrada Esperanza (FMNH 89118–89121); see table 56 for measurements.

Unvouchered observations: None.

Identification: *Thyroptera lavali* is distinguished from other members of the genus by the following combination of characteristics: bicolored brownish ventral pelage; proximal portion of the forearm sparsely haired; adhesive disk at base of thumb oblong; calcar with just one posterolaterally projecting lappet; foramen ovale large; outer upper incisor mesial and distal cusps subequal in size; both cusps on the outer upper incisor perpendicularly arranged relative to the long axis of the toothrow; first upper premolar circular in occlusal view; and outer lower incisor lacking accessory cusps (Velazco et al., 2014; López-Baucells et al., 2018). Descriptions and measurements of *T. lavali* have been provided by Pine (1993), Solari et al. (2004), Gregorin et al. (2006), and Velazco et al. (2014). No subspecies are currently recognized (Wilson, 2008a).

The type series of *Thyroptera lavali* was comprised of four specimens from Quebrada Esperanza (Pine, 1993). Ascorra et al. (1993) identified the specimen from Jenaro Herrera as *T. discifera,* but Solari et al. (2004) correctly reidentified it as *Thyroptera lavali.*

Remarks: No ecological information is available about *Thyroptera lavali* in our region.

Thyroptera tricolor Spix, 1823

Figure 31A

Voucher material (total = 22): Isla Padre (MUSM 21332), Nuevo San Juan (AMNH 272761, 273155–273157, 273160, 273161; MUSM 13262, 13263, 15278–15282), Orosa (AMNH 74022–74025), Quebrada Esperanza (FMNH 89117), San Fernando (FMNH 89166–89168); see table 57 for measurements.

Unvouchered observations: One individual of *Thyroptera tricolor* was captured at Tapiche during the Sierra del Divisor Rapid Biological Inven-

FIG. 31. Photographs of **A,** an adult *Thyroptera tricolor* captured at Tahuayo Farm; and **B,** an adult (CEBIO-MAS 237) *T. wynneae* captured at Jenaro Herrera. Photographs by Brock Fenton (A) and Burton Lim (B).

TABLE 56

External and Craniodental Measurements (mm) and Weights (g) of *Thyroptera lavali* from the Yavarí-Ucayali Interfluve

	FMNH 89118 ♂	MUSM 5944 ♂	FMNH 89119 ♀	FMNH 89120 ♀	FMNH 89121 ♀
W	—	4.0	—	—	—
ToL	74	70	80	87	87
LT	23	37	30	31	30
HF	6	6	7	7	7
E	8	11	8	8	8
F	39.0	39.0	41.0	40.0	40.0
GLS	15.5	15.2	15.6	15.8	15.4
ZB	8.1	—	—	—	8.0
MTR	6.2	6.2	6.5	6.5	6.5
BAM	5.6	5.5	5.8	5.7	5.8

tory (Jorge and Velazco, 2006), and we captured another at Tahuayo Farm on 22 February 2019.

Identification: *Thyroptera tricolor* is distinguished from other members of the genus by the following combination of characteristics: unicolored white or whitish ventral pelage; proximal portion of the forearm sparsely haired; adhesive disk at base of thumb circular; calcar with two posterolaterally projecting lappets; foramen ovale large; outer upper incisor with mesial cusp larger than distal cusp; both cusps on outer upper incisor obliquely arranged relative to long axis of the toothrow; first upper premolar circular in occlusal view; and outer lower incisors with two weakly developed accessory cusps (mesostyle and distostyle) (Velazco et al., 2014; López-Baucells et al., 2018). Descriptions and measurements of *T. tricolor* were provided by Wilson and Findley (1977), Pine (1993), Solari et al. (2004), Bezerra et al. (2005), Lim et al. (2005), Gregorin et al. (2006), Velazco et al. (2014), Velazco and Patterson (2019), and Semedo et al. (2020). Three subspecies are currently recognized: *T. t. albiventer* (southern Mexico to Colombia and Ecuador), *T. t. juquiaensis* (southeastern Brazil), and *T. t. tricolor* (northern Bolivia, eastern Peru, Amazonian Brazil, Venezuela, and the Guianas) (Vieira, 1955; Wilson, 2008a). All the specimens from the Yavarí-Ucayali interfluve that we examined are morphologically and morphometrically indistinguishable from conspecific material from French Guiana (Simmons and Voss, 1998), Brazil (e.g., AMNH 94550, 97131), Ecuador (e.g., AMNH 67592), Trinidad (e.g., AMNH 185342, 29693; FMNH 53054), Venezuela (e.g., AMNH 77556, 77558), and Costa Rica (e.g., FMNH 43980). In the absence of any clear pattern of geographical variation, we recommend against recognizing subspecies of *T. tricolor* until more comprehensive studies based on larger sample sizes and genetic data are completed.

Fleck et al. (2002) correctly identified their specimens from Nuevo San Juan as *Thyroptera tricolor.*

Remarks: We captured *Thyroptera tricolor* only twice in ground-level mistnets near Nuevo San Juan, once in primary upland forest and once in a palm swamp (*aguajal*). By contrast, we found six roosts of this species at the same locality (table 58), all of them in the rolled new leaves of large *Heliconia* sp. (Heliconiaceae) about 3.5–4.5 m above the ground in young secondary growth (recently abandoned swiddens). Although most of the bats in these roosts escaped, all appeared to be *T. tricolor,* which we never found roosting with other species. At Tahuayo Farm, we found two

TABLE 57

External and Craniodental Measurements (mm) and Weights (g) of *Thyroptera tricolor* from the Yavarí-Ucayali Interfluve

	Males[a]	Females[b]
W	4.6 (4.0–5.1) 6	4.5 (3.5–5.1) 7
ToL	72.1 (67–75) 7	73.5 (69–79) 8
LT	28.6 (25–30) 7	27.4 (25–30) 8
HF	5.6 (4–6) 9	5.5 (4–6) 9
E	12.0 (10–13) 7	12.4 (12–13) 7
F	37.1 (35.4–40.0) 9	36.8 (35.0–38.0) 9
GLS	14.4 (14.2–14.8) 4	14.6 (14.2–14.9) 6
CIL	13.8 (13.5–14.3) 3	13.8 (13.6–14.0) 6
ZB	7.6 (7.4–7.7) 4	7.5 (7.4–7.6) 3
MTL	5.9 (5.8–6.0) 4	6.0 (5.8–6.2) 6
BAM	5.2 (5.1–5.4) 4	5.4 (5.3–5.5) 6

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74022, 273157, 273161; FMNH 89166–89167; MUSM 13262, 15279–15281, 21332.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74024–74025, 272761, 273155–273156, 273160; FMNH 89117, 89168; MUSM 13263, 15278, 15282.

individuals of this species roosting in a rolled new leaf of an unidentified *Heliconia*; one individual escaped, but the other, an adult female, was captured and definitely identified.

Although thyropterids in general are sometimes said to roost in the half-unrolled new leaves of large monocots (Findley and Wilson, 1974), *Thyroptera tricolor* is, in fact, the only thyropterid definitely known to do so (Velazco et al., 2014), and even this species sometimes uses other refugia (such as rolled-up dead leaves; Simmons and Voss, 1998: fig. 54). However, the roosts in which we found *T. tricolor* at Nuevo San Juan were typical of the species.

Thyroptera wynneae Velazco et al., 2014

Figure 31B

Voucher material (total = 1): Jenaro Herrera (CEBIOMAS 237); see table 55 for measurements.

Unvouchered observations: None.

Identification: Jenaro Herrera is the type locality of *Thyroptera wynneae*, which can be distinguished from other congeners by the following combination of traits: tricolored brownish ventral pelage; proximal portion of the forearm well furred; adhesive disk at base of thumb oblong; calcar with two posterolaterally projecting lappets plus five tiny skin projections between the foot disk and the proximal lappet; foramen ovale large; outer upper incisor mesial cusp larger than the distal cusp; both cusps on the outer upper incisor perpendicularly arranged relative to the long axis of the toothrow; first upper premolar circular in occlusal view; and outer lower incisor with two small accessory cusps (mesostyle and distostyle) (Velazco et al., 2014; López-Baucells et al., 2018). Descriptions and measurements of *T. wynneae* were provided by Velazco et al. (2014) and Hoppe et al. (2014). No subspecies are currently recognized (Velazco et al., 2014).

Remarks: We found a single roosting group of *Thyroptera wynneae* near Jenaro Herrera, where two individuals (of which one adult male was collected) were discovered inside a dead *Cecropia* leaf hanging by its petiole about 2 m

TABLE 58

Roosting Groups of *Thyroptera tricolor* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
16 Oct 1999	unmodified foliage	about 7	no	1 ad. female
16 Oct 1999	unmodified foliage	about 12	no	1 ad. male, 1 ad. female
16 Oct 1999	unmodified foliage	about 7	no	1 ad. male, 1 ad. female
16 Oct 1999	unmodified foliage	4	no	1 ad. male
18 Oct 1999	unmodified foliage	about 12	no	1 ad. male, 1 ad. female
19 Oct 1999	unmodified foliage	about 9	no	1 ad. male, 1 ad. female

above the ground in secondary vegetation on 29 January 2012 (Velazco et al., 2014: fig. 8).

Family Vespertilionidae Gray 1821

Members of the cosmopolitan family Vespertilionidae are characterized by plain faces lacking a noseleaf; relatively small eyes; wing digit II reduced to the metacarpal plus a single small phalanx; and a long tail that reaches the edge of the uropatagium, and which is entirely enclosed within that membrane (Koopman, 1994; Reid, 2009; López-Baucells et al., 2018). Eight vespertilionid species in three genera (*Eptesicus*, *Lasiurus*, and *Myotis*) are expected to occur in the Yavarí-Ucayali interfluve (Davis and Gardner, 2008; Gardner and Handley, 2008; Wilson, 2008b; Moratelli et al., 2013), of which seven were captured and one (*Lasiurus blossevillii*) was detected by acoustic methods.

Eptesicus Rafinesque, 1820

The genus *Eptesicus* is nearly worldwide in distribution and includes 35 currently recognized species (Simmons, 2005; Simmons and Cirranello, 2020). These bats are characterized by medium to large size; a large premolar adjacent to the upper canine (no gap in the toothrow behind the canine); well-developed upper incisors with the inner teeth larger than the outer teeth; and three subequal, trifid lower incisors, the third of which has a wider crown than either of the first two (Miller, 1907; Davis and Gardner, 2008; Reid, 2009; Sánchez et al., 2019). Davis and Gardner (2008) provided a key to the New World species of the genus. During the 2012 CEBIO bat course, three acoustic forms of *Eptesicus* were detected (*E. brasiliensis*, *E.* cf. *brasiliensis*, and *E.* cf. *furinalis*), but only two species (*E. brasiliensis* and *E. furinalis*) have been collected in the Yavarí-Ucayali interfluve. Based on range maps only *E. brasiliensis* and *E. furinalis* are expected to occur in our region, so it is not clear whether the third acoustic form detected in 2012 represents an unrecognized species or aberrant calls of *E. brasiliensis*.

Eptesicus brasiliensis (Desmarest, 1819)

Voucher material (total = 4): Jenaro Herrera (MUSM 5596, 5597), Nuevo San Juan (MUSM 13201), Quebrada Sábalo (MUSA 15237); see table 59 for measurements.

Unvouchered observations: None.

Identification: *Eptesicus brasiliensis* is distinguished from other Neotropical congeners by its medium size (forearm 40–47 mm, greatest length of skull 16–18 mm), relatively short (<7 mm) dorsal fur, brownish ventral fur, U-shaped nasal opening, and inflated rostrum (Davis, 1966; Miranda et al., 2006; Davis and Gardner, 2008; López-Baucells et al., 2018). Descriptions and measurements of *E. brasiliensis* were provided by Davis (1965, 1966), Barquez et al. (1999), Lim et al. (2005), Miranda et al. (2006),

TABLE 59

External and Craniodental Measurements (mm) and Weights (g) of *Eptesicus brasiliensis* and *E. furinalis* from the Yavarí-Ucayali Interfluve

	E. brasiliensis		*E. furinalis*	
	MUSM 13201 ♂	Females[a]	ROM 122089 ♂	ROM 122178 ♀
W	10	11, 11, 8	10	9
ToL	105	104, 101, 100	99	102
LT	41	41, 45, 41	44	48
HF	10	9, 8, 10.5	10	9
E	15	14, 14, 15	13	14
F	43.0	44.6, 44.4, 43.0	41.0	41.0
GLS	16.4	16.2, 16.0, –	15.9	16.6
CIL	15.9	15.7, 15.8, –	15.3	15.9
BB	7.5	7.7, 7.7, –	7.6	7.4
MB	8.6	8.7, 9.0, –	8.8	8.7
ZB	11.1	11.2, 11.7, –	11.3	11.4
MTL	6.5	6.1, 6.1, –	5.9	5.8
BAM	7.1	6.8, 7.2, –	7.3	7.0

[a] MUSM 5596, 5597; MUSA 15237.

Davis and Gardner (2008), and Sánchez et al. (2019). Four subspecies are currently recognized: *E. b. arge* (northern Argentina, southern Brazil, Paraguay, and Uruguay), *E. b. brasiliensis* (eastern Brazil), *E. b. melanopterus* (lowlands of Colombia, Guyana, Surinam, Venezuela, and the Amazon basin of Brazil), and *E. b. thomasi* (western Amazon basin of eastern Ecuador and Peru) (Davis and Gardner, 2008). Based on distribution, our voucher material from the Yavarí-Ucayali interfluve should correspond to *E. b. thomasi.* However, most of the characteristics noted by Davis (1966) as diagnostic of *E. b. thomasi* are measurements that overlap those of other subspecies, and in our experience populations of *E. brasiliensis* are highly variable. Until comprehensive studies including larger sample sizes and genetic data became available, we recommend against formally recognizing subspecies.

Ascorra et al. (1993) and Fleck et al. (2002) correctly identified their specimens from Jenaro Herrera and Nuevo San Juan, respectively. The voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Eptesicus brasiliensis*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: The only recorded capture of *Eptesicus brasiliensis* accompanied by ecological information from our region is an adult male that we found beneath a sheet of exfoliating bark on the underside of a fallen tree about 50 cm above the ground in a Matses swidden near Nuevo San Juan on 31 May 1998. One individual of *Myotis albescens* was found roosting beneath another sheet of bark on the same fallen tree at the same time. Both bats were torpid when this roost was discovered in midafternoon.

Eptesicus furinalis
(d'Orbigny and Gervais, 1847)

Figure 32

Voucher material (total = 2): Jenaro Herrera (ROM 122089, 122178); see table 59 for measurements.

FIG. 32. Photograph of an adult *Eptesicus furinalis* captured at Frog Valley. Photograph by Brock Fenton.

Unvouchered observations: We captured six individuals of *Eptesicus furinalis* between 16 and 21 February 2019 on the Tahuayo expedition, five at El Chino Village and one at Frog Valley. This species was also identified using acoustic methods during the CEBIO bat course at Jenaro Herrera in 2012.

Identification: *Eptesicus furinalis* can be distinguished from other Neotropical congeners by its medium size (forearm 36–43 mm, greatest length of skull >15 mm), relatively short (<7 mm) dorsal fur, and yellowish ventral fur (Davis, 1966; Davis and Gardner, 2008; López-Baucells et al., 2018). Descriptions and measurements of *Eptesicus furinalis* have been provided by Davis (1966), Barquez et al. (1999), Lim et al. (2005), Davis and Gardner (2008), and Sánchez et al. (2019). Two subspecies are currently recognized: *E. f. furinalis* (northern Argentina, Paraguay, Bolivia, Brazil, and Uruguay) and *E. f. gaumeri* (Mexico southward throughout Central America to Amazonian Brazil and Bolivia) (Davis and Gardner, 2008). Based on geography, material from the Yavarí-Ucayali interfluve should correspond to *E. f. gaumeri*, but this species is highly variable across its distribution, and the last revision of the genus (Davis, 1966) did not include any Peruvian samples. Until larger samples and genetic data become available, we recommend against formally recognizing subspecies of *E. furinalis*.

The two specimens from Jenaro Herrera conform to previous descriptions of *Eptesicus furinalis*, with measurements that fall within the range of size variation previously documented for the species. The material we examined in the field at El Chino Village conformed to previous descriptions of the species, with yellowish ventral fur and external measurements that were within the range of size variation previously documented for *Eptesicus furinalis*.

Remarks: Of the eight recorded captures of *Eptesicus furinalis* from our region, three were taken in ground-level mistnets, two were taken in elevated nets, and three were taken in harp traps. Two captures were in primary forest and six were in clearings.

Genus *Lasiurus* Gray, 1831

The systematics of *Lasiurus* has been the focus of numerous studies, and there is persistent controversy as to whether three genera (*Aeorestes*, *Dasypterus*, and *Lasiurus*), two genera (*Dasypterus* and *Lasiurus*), or only one genus (*Lasiurus*) should be recognized (Allen, 1894; Miller, 1907; Tate, 1942; Handley, 1960; Hoofer and Van Den Bussche, 2003; Roehrs et al., 2010; Baird et al., 2015, 2017; Ziegler et al., 2016). Recently, Baird et al. (2015, 2017) argued for recognition of three genera based on analyses of genetic data indicating reciprocal monophyly. In contrast, Ziegler et al. (2016) and Novaes et al. (2018) argued that taxonomic stability was better served by treating *Aeorestes* and *Dasypterus* as subgenera of *Lasiurus*. We concur with the latter authors and use *Lasiurus* as the generic name for all these taxa. Thus defined, *Lasiurus* includes 19 currently recognized species that can be distinguished from members of other vespertilionid genera by having long, dense fur covering the proximal third or more of the upper surface of the uropatagium; a short, deep rostrum; one pair of upper incisors; and right and left premaxillae separated by a

palatal emargination that is approximately one-third the distance across the canines (Gardner and Handley, 2008; López-Baucells et al., 2018; Simmons and Cirranello, 2020).

During the 2012 CEBIO bat course, two acoustic forms of *Lasiurus* were detected (*Lasiurus* sp. and *L. blossevillii*). Based on range maps, only *L. blossevillii* and *L. ega* are expected to occur in the Yavarí-Ucayali interfluve (Gardner and Handley, 2008). Because we captured *L. ega* at El Chino Village, the unidentified calls detected at Jenaro Herrera most likely belonged to this species.

Lasiurus (*Dasypterus*) *ega* (Gervais, 1856)

Figure 33

Voucher material: None.

Unvouchered observations: We captured 10 individuals of *Lasiurus ega* at El Chino Village between 18 and 21 February 2019.

Identification: *Lasiurus ega* is a widespread species distributed from the southern United States to northern Argentina (Kurta and Lehr, 1995; Gardner and Handley, 2008). This species can be distinguished from other congeners by its yellowish dorsal and ventral fur, lack of pelage frosting, black dactylopatagium, and presence of only one upper premolar (Gardner and Handley, 2008; López-Baucells et al., 2018). Descriptions and measurements of *L. ega* have been provided by Husson (1962, 1978), Kurta and Lehr (1995), Gardner and Handley (2008), and Giménez and Giannini (2011). Four subspecies are currently recognized: *L. e. argentinus* (Paraguay, Uruguay, southern Bolivia, southeastern Brazil, and northern Argentina); *L. e. ega* (throughout most of tropical South America east of the Andes); *L. e. fuscatus* (western Colombia and Ecuador); and *L. e. panamensis* (Texas to northern Colombia and northwestern Venezuela) (Gardner and Handley, 2008).

The specimens we examined from El Chino Village were unambiguously identified as *Lasiurus ega* based on external characters.

Remarks: Of the 10 individuals of *Lasiurus ega* captured at El Chino, two were taken 5–10 m above the ground in a macro net, and the rest were taken by hand from roosts about 3 m above the ground in the palm-frond roof thatch of a pavilion in the village plaza (fig. 33B). The first group, captured on 18 February 2019, consisted of three females that were roosting tightly packed together about 30 cm up inside the edge of the thatch, but clearly visible from the ground. The second and third groups, captured on 21 February 2019 under similar circumstances, consisted of three individuals (all females) and two individuals (one male and one female) respectively.

Genus *Myotis* Kaup, 1829

The genus *Myotis* is the most widely distributed bat genus and contains more than 120 species worldwide (Gunnell et al., 2017; Simmons and Cirranello, 2020). Species of *Myotis* can be distinguished from other vespertilionids by the presence of two pairs of upper incisors, three premolars in each toothrow, extreme differences in size between the anterior premolars and the posterior premolar (which creates an apparent gap in the toothrow behind the canine when viewed laterally), and by the tendency for the upper second premolar to be displaced lingually, so that the distance between the first and third premolars is reduced (Tate, 1941; López-Baucells et al., 2018). The taxonomy and systematics of Neotropical *Myotis* have been the focus of numerous studies based either on morphological data (e.g., Wilson, 2008b; Moratelli and de Oliveira, 2011; Moratelli et al., 2011a, b, 2013; Moratelli and Wilson, 2011, 2014a; Mantilla-Meluk and Muñoz-Garay, 2014) or molecular sequence analyses (e.g., Ruedi and Mayer, 2001; Bickham et al., 2004; Stadelmann et al., 2007; Larsen et al., 2012). Different types of data and geographic coverage have produced results that are not entirely congruent with each other, so considerable taxonomic uncertainty remains. We recorded all four species of *Myotis* with geographic ranges that overlap the Yavarí-Ucayali interfluve.

FIG. 33. Photographs of **A,** an adult *Lasiurus ega* captured at El Chino Village and **B,** two individuals of *L. ega* roosting under a palm-frond roof thatch at El Chino Village. Photographs by Brock Fenton.

FIG. 34. Photographs of **A,** an adult *Myotis albescens* captured at Jenaro Herrera; **B,** an adult *M. nigricans* captured at El Chino Village; and **C,** an adult *M. riparius* captured at Jenaro Herrera. Photographs by Marco Tschapka (A, C) and Brock Fenton (B).

TABLE 60

External and Craniodental Measurements (mm) and Weights (g) of *Myotis albescens* and *M. nigricans* from the Yavarí-Ucayali Interfluve

	M. albescens		*M. nigricans*	
	Males[a]	Females[b]	Males[c]	Females[d]
W	5.0 (3.0–6.3) 3	5.6	4, –	5.0, 4.2
ToL	77.0 (68–87) 3	91	81, –	88, 76
LT	33.3 (30–36) 3	38	38, –	38, 34
HF	8.3 (7–9) 3	9	7, 8	7, 6
E	13.7 (13–14) 3	13	12, –	11, 18
F	(33.0) 3	35.0	34.1, 34.3	34.3, 35.1
GLS	13.6	13.6 (13.4–13.8) 4	13.6, –	13.6, 13.4
CIL	13.1	12.9 (12.7–13.0) 4	13.2, –	13.1, 12.8
BB	6.5 (6.2–6.8) 2	6.9 (6.7–7.1) 6	6.8, –	6.6, 6.4
MB	7.0 (6.8–7.2) 2	7.1 (7.0–7.3) 3	7.2, –	7.2, 7.0
ZB	8.5	8.3	8.5, –	8.6, 8.3
MTL	4.8 (4.6–5.0) 2	5.0 (4.9–5.1) 5	5.2, –	5.1, 5.0
BAM	5.5	5.3 (5.2–5.4) 5	5.6, –	5.4, 5.6

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272707; MUSM 5508, 15240.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74017–74021; MUSM 13222.

[c] MUSM 5602, 23795.

[d] MUSM 5601, 21341.

Myotis albescens (É. Geoffroy St.-Hilaire, 1806)

Figure 34A

Voucher material (total = 9): Jenaro Herrera (MUSM 5508), Nuevo San Juan (AMNH 272707; MUSM 13222, 15240), Orosa (AMNH 74017–74021); see table 60 for measurements.

Unvouchered observations: We captured four individuals of *Myotis albescens* at El Chino Village in February 2019.

Identification: *Myotis albescens* is distinguished from other Neotropical *Myotis* by the following combination of characteristics: fur long and silky, dorsal pelage with frosted appearance due to pale-tipped hairs, fringe of hairs present along the trailing edge of uropatagium, sagittal crest absent, broad interorbital and postorbital constrictions, and a globular braincase (LaVal, 1973; López-González et al., 2001; Moratelli and de Oliveira, 2011). Descriptions and measurements of *M. albescens* were provided by Miller (1928), Husson (1962, 1978), Quintela et al. (2008), Braun et al. (2009), Moratelli and de Oliveira (2011), and Moratelli et al. (2013, 2015a). No subspecies are currently recognized (Braun et al., 2009), but analyses of molecular data (cytochrome *b* sequences) suggest the presence of at least four lineages that are >5 % divergent from each other (Larsen et al., 2012); the possibility that these mtDNA haplogroups represent cryptic taxa merits future testing with nuclear-gene sequences or phenotypic data.

Ascorra et al. (1993), Fleck et al. (2002), Moratelli and Oliveira (2011) and Moratelli and Wilson (2011) correctly identified the specimens from Jenaro Herrera, Nuevo San Juan, and Orosa, which conform to previous qualitative and morphometric descriptions of *Myotis albescens*.

Remarks: Four recorded nocturnal captures of *Myotis albescens* are accompanied by ecological data from our region, all of which were made in ground-level mistnets; these include one individual netted in secondary vegetation, two netted in clearings, and one netted over a stream. A single individual was smacked out of the air with a stick by a Matses man as it flew by along the shoreline of the Río Gálvez at dusk.

We found a single roost of *Myotis albescens* near Nuevo San Juan, where a solitary adult male was found beneath a sheet of exfoliating bark on the underside of a fallen tree in a Matses swidden on 31 May 1998. Another roosting group of *Myotis albescens* was found among the rafters supporting the roof of the school at El Chino on 21 February 2019; we captured three adult females (one of which was carrying a pup), but a number of other individuals escaped.

Myotis nigricans (Schinz, 1821)

Figure 34B

Voucher material (total = 5): Jenaro Herrera (MUSM 5601, 5602, 23795, 23796), Quebrada Blanco (MUSM 21341); see table 60 for measurements.

Unvouchered observations: We captured 12 *Myotis nigricans* at El Chino Village and another 3 at Tahuayo Farm.

Identification: As traditionally recognized, *Myotis nigricans* was a species complex, from which Larsen et al. (2012), Moratelli et al. (2013, 2017), and Moratelli and Wilson (2014b) have recently described new species and elevated others from synonymy. Nevertheless, *M. nigricans* (in its current, stricter sense) remains a widespread taxon, ranging from northwestern Mexico to northern Argentina and southern Brazil (Moratelli et al., 2013, 2017; Moratelli and Wilson, 2014b). As now recognized, *M. nigricans* is distinguished from other congeners by the following combination of traits: forearm <36 mm; dorsal pelage long, silky, and bicolored; no fringe of hairs along the trailing edge of the uropatagium; sagittal crest absent or weakly developed; and frontals steeply sloping (Moratelli et al., 2013). Descriptions and measurements of *Myotis nigricans* have been provided by Moratelli et al. (2013) and Moratelli and Wilson (2014b). Two subspecies are currently recognized: *M. n. extremus* (southern Mexico) and *M. n. nigricans* (eastern Mexico throughout tropical and subtropical South America on both sides of the Andes; Moratelli et al., 2013). However, analyses of cytochrome *b* sequence data have discovered >10 mitochondrial lineages within the range of the nominotypical subspecies (Larsen et al. 2012), highlighting the need for additional revisionary research on these bats.

Ascorra et al. (1993) correctly identified their specimens from Jenaro Herrera. The additional voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Myotis nigricans*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: Of 17 specimens of *Myotis nigricans* accompanied by ecological information from our region, 5 were captured in ground-level mistnets and 12 in harp traps; these captures included 4 in secondary vegetation, 12 in clearings, and 1 on a river beach.

Myotis riparius Handley, 1960

Figure 34C

Voucher material (total = 20): Isla Padre (MUSM 4356, 4363), Jenaro Herrera (CEBIOMAS 115; MUSM 5512, 5515, 5520, 5524, 5527, 5532, 5599, 5600, 5603, 6662), Nuevo San Juan (AMNH 272742, 272752; MUSM 13223, 13224), Quebrada Blanco (MUSM 21342, 21343, 21345); see table 61 for measurements.

Unvouchered observations: None.

Identification: *Myotis riparius* is distinguished from other congeners by its long, woolly fur; unicolored dorsal fur; plagiopatagium attached to the foot at base of digit I; fringe of hairs absent along the trailing edge of uropatagium; sagittal and lambdoidal crests forming a triangular "helmet" at their juncture in the interparietal region; and occip-

TABLE 61

External and Craniodental Measurements (mm) and Weights (g) of *Myotis riparius* and *M. simus* from the Yavarí-Ucayali Interfluve

	M. riparius		*M. simus*
	Males[a]	Females[b]	Males[c]
W	5.5 (4.8–7.0) 8	5.3 (4.0–6.2) 8	—
ToL	83.1 (79–88) 8	81.6 (75–86) 8	—
LT	34.5 (30–37) 8	36.0 (35–38) 8	—
HF	6.9 (5–8) 9	6.5 (6–7) 9	—
E	11.9 (11–13) 8	11.6 (10–13) 8	—
F	36.3 (33.0–38.0) 9	36.3 (35.0–37.0) 9	—
GLS	13.4 (13.0–13.7) 9	13.4 (13.2–13.7) 8	13.4, 14.4
CIL	13.1 (12.8–13.5) 8	13.2 (12.7–13.8) 7	13.2, 14.0
BB	6.5 (6.1–7.0) 9	6.5 (6.2–6.7) 8	7.2
MB	7.1 (6.8–7.5) 9	7.1 (6.9–7.3) 7	7.5, 7.8
ZB	9.0 (8.9–9.0) 4	9.0 (8.8–9.2) 5	—
MTL	5.2 (5.1–5.4) 9	5.1 (5.0–5.3) 8	5.1 (5.0–5.4) 3
BAM	5.7 (5.6–5.8) 9	5.7 (5.4–6.0) 9	5.7 (5.6–5.8) 3

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272742, 272752; MUSM 4363, 5512, 5515, 5527, 5599, 13223–13224, 21342.
[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of CEBIOMAS 115; MUSM 4356, 5520, 5524, 5532, 5600, 5603, 6662, 21343, 21345.
[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 74105, 74109–74110.

ital region flattened posteriorly (Handley, 1960; Novaes et al., 2017). Descriptions and measurements of *M. riparius* were provided by Handley (1960), LaVal (1973), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Lim et al. (1999, 2005), López-González et al. (2001), Moratelli et al. (2013), Novaes et al. (2017), and Velazco and Patterson (2019). No subspecies are currently recognized (Novaes et al., 2017), but molecular data suggest the presence of cryptic diversity, and a comprehensive revision of the species is needed (Larsen et al., 2012).

Ascorra et al. (1993) identified their specimens from Jenaro Herrera either as *Myotis riparius* (MUSM 5603, 5212, 5215) or *M. simus* (MUSM 5520, 5524, 5599, 5600). Fleck et al. (2002) correctly identified their specimens from Nuevo San Juan. The voucher material that we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions of *M. riparius*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: All of the nine recorded captures of *Myotis riparius* accompanied by ecological information from our region were taken in ground-level mistnets, seven of them in primary forest and two in secondary vegetation.

Myotis simus Thomas, 1901

Voucher material (total = 3): Orosa (AMNH 74105, 74109, 74110); see table 61 for measurements.

Unvouchered observations: None.

Identification: The primary diagnostic characteristic of *Myotis simus* is the attachment

of the plagiopatagium at the ankle or at the level of the toes by a narrow (<1.5 mm wide) band of membrane (López-González et al., 2001). Additionally, *M. simus* has short (<4 mm), woolly fur; lacks a fringe of hairs along the trailing edge of the uropatagium; sagittal and lambdoidal crests are present; and the occipital region is flattened posteriorly (Moratelli, 2012). Descriptions and measurements of *M. simus* were provided by Miller (1928), Handley (1960), LaVal (1973), Carter and Dolan (1978), López-González et al. (2001), Wilson (2008b), Moratelli (2012), Moratelli et al. (2011a, 2013, 2015b), and Moratelli and Wilson (2014a). No subspecies are currently recognized (Moratelli, 2012), but a revision is needed due to the suspected presence of cryptic molecular diversity within this taxon as currently recognized (Larsen et al., 2012).

Moratelli et al. (2013) identified the material from Orosa as *Myotis simus*, and we agree that these specimens conform to previous descriptions and measurements of the species.

Remarks: No ecological information is available about this species in our region.

Family Molossidae Gervais, 1856

The nearly cosmopolitan family Molossidae (commonly known as free-tailed bats) is the fourth most diverse family of bats with more than 100 species worldwide, most of which occur in tropical regions (Simmons, 2005; Gregorin and Cirranello, 2016; Simmons and Cirranello, 2020). Molossids are characterized morphologically by a reduced tragus, a (usually) large antitragus, a pinna that lacks a basal lobe, a skull that lacks postorbital processes, a humerus with a trochiter much larger than the trochin, and a seventh cervical vertebra that is fused with the first thoracic vertebra (Miller, 1907). All Amazonian molossids belong to the subfamily Molossinae, which is characterized morphologically by long, narrow wings; tough, leathery wing and tail membranes; a thick tail that extends well beyond the posterior margin of the uropatagium; short, robust legs; short, broad feet provided with long sensory hairs; a reduced tragus; and a large antitragus (Eger, 2008). Of all the species expected to occur in the Yavarí-Ucayali interfluve, molossids are the least well represented in our voucher material due to the challenge of capturing these high-flying bats. Whereas 17 molossid species have geographic ranges that overlap our region, only seven are documented by locally collected voucher material, although two others (*Nyctinomops* cf. *macrotis* and *Promops nasutus*) were provisionally identified using acoustic methods.

Cynomops planirostris (Peters, 1866)

Figure 35

Voucher material (total = 1): Jenaro Herrera (AMNH 278460); see table 62 for measurements.

Unvouchered observations: Four additional individuals were captured at Jenaro Herrera during the CEBIO bat course on 22 January 2012.

Identification: *Cynomops*, once treated as a subgenus of *Molossops* but now ranked as a distinct genus, ranges throughout most of the Neotropics and is currently thought to include eight species (Moras et al., 2016, 2018; Simmons and Cirranello, 2020). Moras et al. (2016) reviewed the taxonomy and systematics of *Cynomops*, and Moras et al. (2018) provided a helpful key to the species.

Moras et al. (2016) recommended that *Cynomops paranus* should be considered a junior synonym of *C. planirostris* contra Williams and Genoways (1980b), Barquez et al. (1993), and Simmons and Voss (1998), and we concur with that assessment. Thus defined, *C. planirostris* (including *paranus*) is widely distributed in tropical and subtropical South America east of the Andes (dos Santos et al., 2015; Moras et al., 2016). It can be distinguished from other congeneric species by external and craniodental features including small size (forearm 29–37 mm, greatest length of skull 14–17 mm), bicolored dorsal fur (varying from chocolate brown to

FIG. 35. Photographs of an adult *Cynomops planirostris* captured at Jenaro Herrera. Photograph by Marco Tschapka.

grayish brown), paler (whitish or pale buff) ventral pelage, anterior edge of the lacrimal ridge sloping smoothly to the forehead, incisive foramina in close proximity to the accessory foramen (the three foramina forming an equilateral triangle), shallow basisphenoid pits, and presence of a well-developed median ridge on the lingual face of the second lower premolar (Moras et al., 2016, 2018). Descriptions and measurements of this species (in a variety of binomial and trinomial combinations; see above) have been provided by Husson (1962, 1978), Carter and Dolan (1978), Simmons and Voss (1998), Lim and Engstrom (2001a), Díaz (2011), Giménez and Giannini (2016), and Moras et al. (2016, 2018). No subspecies are currently recognized (Moras et al., 2016).

Our single specimen from the Yavarí-Ucayali interfluve conforms to previous descriptions of *Cynomops planirostris*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: One individual of *Cynomops planirostris* from our region was captured in an elevated mistnet in a clearing, and the other four were taken in ground-level mistnets over a stream.

Genus *Eumops* Miller, 1906

The widespread genus *Eumops* includes 17 currently recognized species (Simmons and Cirranello, 2020). Traits that distinguish this genus from other molossids include large, rounded pinnae that are joined across the forehead and have a greatly developed keel, reduced and pointed or square-tipped tragus, and a large, nearly oval antitragus; smooth (unwrinkled) upper lips; cylindrical skull; well-developed basisphenoid pits; slightly arched palate; long, curved upper incisors; and M3 with a variably developed

TABLE 62

External and Craniodental Measurements (mm) and Weights (g) of *Cynomops planirostris*, *Eumops hansae* and *Molossops neglectus* from the Yavarí-Ucayali Interfluve

	C. planirostris	*E. hansae*		*M. neglectus*	
	AMNH 278460 ♂	Males[a]	MUSA 15144 ♀	Males[b]	MUSM 6972 ♀
W	12.5	14, 10	11.0	14.0, 16.0	9.6
ToL	87	99, 90	93	104, 95	85
LT	21	29, 27	27	34, 30	27
HF	9	10, 8	10	8, 6	8
E	14	17, 21	16	18, 15	18
F	33.0	37.6, 38.8	37.2	39.0, 38.2	37.3
GLS	16.1	18.7, 18.0	17.7	17.1, 17.2	15.8
CIL	16.7	18.3, 17.6	17.2	17.5, 17.4	15.8
PB	4.6	4.0, 4.2	4.1	4.7, 4.5	4.4
BB	8.1	8.6, 8.8	8.5	8.6, 8.9	8.3
MB	10.2	9.4, 10.3	9.3	11.5, 11.1	9.9
ZB	10.8	10.8, –	10.4	–, 12.0	—
MTL	6.6	7.0, 6.9	6.7	7.2, 6.9	6.4
BAM	7.3	7.9, 7.4	7.7	8.4, 8.2	7.6

[a] MUSA 15193, 20982.
[b] MUSM 5517, 6573.

third commissure (Eger, 2008; Medina et al., 2014). Eger (1977, 2008) and Gregorin (2009) reviewed the taxonomy and systematics of the genus, and Eger (2008) provided a key to the species based on external and cranial characters. Three acoustic forms of *Eumops* were detected during the 2012 CEBIO bat course at Jenaro Herrera, of which only *E. hansae* is documented with voucher material collected in the Yavarí-Ucayali interfluve (the other two acoustic taxa remain unidentified). Five other congeners expected to occur in our region are listed in appendix 2.

Eumops hansae Sanborn, 1932

Voucher material (total = 3): Quebrada Betilia (MUSA 15193), Quebrada Blanco (MUSM 20982), Quebrada Lobo (MUSA 15144); see table 62 for measurements.

Unvouchered observations: During the CEBIO bat course in Jenaro Herrera, *Eumops hansae* was recorded using acoustic methods.

Identification: *Eumops hansae* can be distinguished from other congeneric species by the following combination of characteristics: medium size (forearm 37–41 mm); short, blackish brown dorsal fur; white-based ventral fur; greatest length of skull ca. 50% of forearm length; and long, deep basisphenoid pits (Eger, 2008). Descriptions and measurements of *E. hansae* were provided by Sanborn (1932), Gardner et al. (1970), Eger (1977, 2008), Brosset and Charles-Dominique (1990), Simmons and Voss (1998), Gregorin (2009), and Medina et al. (2012). No subspecies are currently recognized (Eger, 2008).

Medina et al. (2015) correctly identified their specimens from Quebrada Betilia and Quebrada Lobo as *Eumops hansae*. The voucher material we examined from the Yavarí-Ucayali interfluve

conforms to previous descriptions and measurements of the species.

Remarks: No ecological information is available about this species from our region.

Molossops neglectus Williams and Genoways, 1980

Figure 36

Voucher material (total = 4): Jenaro Herrera (CEBIOMAS 89; MUSM 5517, 6573, 6972); see table 62 for measurements.

Unvouchered observations: None.

Identification: *Molossops* is a Neotropical genus with just two species (Gregorin et al., 2004; Eger, 2008; Simmons and Cirranello, 2020). *Molossops neglectus* can be distinguished from *M. temminckii* by its larger size (forearm >35 mm) and from species in other molossid genera by the following combination of the traits: relatively large tragus (at least ½ the size of the antitragus); a short, wide antitragus (wider than high and notched posteriorly); elongated and pointed ears that have a flexible fold where they join the head; well-developed basisphenoid pits; one pair of lower incisors; and M3 with three well-developed commissures (Gregorin et al., 2004; Eger, 2008). Descriptions and measurements of *Molossops neglectus* were provided by Williams and Genoways (1980b), Ascorra et al. (1991b), Barquez et al. (1999), Lim and Engstrom (2001b), Gregorin et al. (2004), Bernardi et al. (2007), Eger (2008), Gregorin and Loureiro (2011), Giménez and Giannini (2016), and Althoff et al. (2018). No subspecies are currently recognized (Eger, 2008).

Ascorra et al. (1993) correctly identified the MUSM specimens from Jenaro Herrera. The other voucher material we examined conforms to previous descriptions of *Molossops neglectus*, with measurements that fall within the range of size variation previously documented for the species.

Remarks: The single specimen of *Molossops neglectus* accompanied by ecological data from our region was taken in an elevated net over a clearing.

Genus *Molossus* É. Geoffroy St.-Hilaire, 1805

The genus *Molossus* includes 14 currently recognized species that collectively range from Mexico to southern Argentina (Loureiro et al., 2020). The genus has been reviewed by Miller (1913b), Dolan (1989), and Loureiro et al. (2018a, b, 2019, 2020). Species of *Molossus* can be distinguished from other molossids by their minute tragus; an antitragus that is constricted at its base; short, rounded ears that arise from the same point on the forehead; smooth (unwrinkled) upper lips; a snout that lacks a prominent median ridge behind the nostrils; a well-developed sagittal crest (better developed in males than in females); an obtusely angled rostrum; arched palate; and divergent upper incisors in line with the canines (Eger, 2008; Gregorin and Cirranello, 2016). All three *Molossus* species expected to occur in the Yavarí-Ucayali interfluve are represented by specimens collected in our region.

Molossus coibensis Allen, 1904

Voucher material (total = 6): Jenaro Herrera (ROM 122087, 122091, 122130, 122177, 122254, 122255); see table 63 for measurements.

Unvouchered observations: None.

Identification: *Molossus coibensis*, which is now known to include *M. barnesi* (see Catzeflis et al., 2016; Loureiro et al., 2019), is distinguished from other congeneric species by its small size (forearm 33–38 mm, greatest length of skull 15–17 mm); short (<3.5 mm), unicolored dorsal fur varying from cocoa-brown to blackish; quadrangular occipital complex; and upper incisors with convergent tips (Eger, 2008; Loureiro et al., 2018a). Descriptions and measurements of the species (as *M. coibensis* or *M. barnesi*) were provided by Dolan (1989), Simmons and Voss (1998), Lim and Engstrom (2001b), Díaz (2011), Catzeflis et al. (2016), and Loureiro et al. (2018a, b, 2019). No subspecies are currently recognized (Eger, 2008).

Loureiro et al. (2018b) correctly identified the specimens from Jenaro Herrera, which conform

FIG. 36. Photographs of an adult *Molossops neglectus* captured at Jenaro Herrera with **(A)** mouth closed and **(B)** mouth open 90°. Photographs by Marco Tschapka.

TABLE 63

External and Craniodental Measurements (mm) and Weights (g) of *Molossus coibensis* and *M. molossus* from the Yavarí-Ucayali Interfluve

	M. coibensis		*M. molossus*	
	ROM 122130 ♂	Females[a]	Males[b]	Females[c]
W	17.0	14.3 (13.5–15.0) 5	16.5 (12.0–20.0) 10	15.3 (12.0–20.0) 11
ToL	93	95.6 (90–99) 5	109.5 (100–115) 10	106.8 (97–116) 12
LT	39	34.0 (30–36) 5	40.4 (36–45) 10	39.5 (36–44) 12
HF	12	9.2 (7–10) 5	9.9 (8–12) 10	9.8 (7–12) 12
E	19	13.2 (12–14) 5	13.6 (12–15) 10	14.1 (12–18) 12
F	38.0	36.0 (35.0–37.0) 5	41.4 (40.0–42.2) 10	41.2 (40.0–43.0) 11
GLS	16.5	16.3 (16.2–16.5) 3	17.3 (17.0–17.6) 5	16.9 (16.7–17.1) 5
CIL	15.4	15.0 (14.8–15.1) 3	16.4 (16.0–16.6) 5	15.9 (15.6–16.1) 5
PB	3.9	3.9 (3.9–4.0) 3	3.8 (3.5–4.0) 5	3.8 (3.6–4.0) 5
BB	9.2	9.1 (9.1–9.2) 3	9.1 (8.8–9.2) 5	8.9 (8.8–9.2) 5
MB	—	10.5 (10.4–10.5) 3	10.6 (10.4–10.7) 5	10.3 (9.9–10.7) 5
ZB	10.7	10.3, 10.8	11.1 (10.8–11.3) 5	10.7(10.4–11.1) 4
MTL	5.9	5.8 (5.7–6.0) 3	6.4 (6.3–6.5) 5	6.3 (6.1–6.4) 5
BAM	7.8	7.8 (7.7–7.9) 3	7.9 (7.8–8.1) 5	7.7 (7.4–8.2) 5

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of ROM 122087, 122091, 122177, 122254, 122255.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272743, 272777, 272778, 278458; CEBIOMAS 90; MUSM 5943, 6663, 13218, 13220, 20983.

[c] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 272744, 272776, 272779, 273115; MUSM 5536, 6664–6666, 6978, 13219, 13221, 15234.

to previous descriptions and measurements of *Molossus coibensis*.

Remarks: Four recorded captures of *Molossus coibensis* accompanied by ecological data from our region were all taken in elevated nets; three captures were in clearings, and one was in secondary vegetation.

Molossus molossus (Pallas, 1766)

Figure 37A

Voucher material (total = 26): Jenaro Herrera (AMNH 278458; CEBIOMAS 90; MUSM 5536, 5943, 6663–6666, 6978), Nuevo San Juan (AMNH 272743, 272744, 272776–272779, 273115; MUSM 13218–13221, 15234), Quebrada Blanco (MUSM 20983), Quebrada Sábalo (MUSA 15226, 15227), Río Blanco (MUSA 15077, 15078); see table 63 for measurements.

Unvouchered observations: Many dozens of *Molossus molossus* were captured and released at Jenaro Herrera during the 2012 CEBIO bat course, and we captured another 15 individuals at El Chino Village in 2019.

Identification: *Molossus molossus* is a widespread taxon that belongs to a species complex with several other taxa previously treated as subspecies or synonyms; in its current, strict sense, *M. molossus* is now thought to range from southern Mexico to northern Argentina, including the Lesser Antilles (Loureiro et al., 2018a, 2019). *Molossus molossus* is distinguished from other congeneric species by its medium size (forearm 35–43 mm, greatest length of skull 15–19 mm);

FIG. 37. Photographs of **A,** an adult *Molossus molossus* and **B,** an adult *M. rufus*, both captured at Jenaro Herrera. Photographs by Marco Tschapka.

long (>4 mm), bicolored dorsal fur, varying from cinnamon to cocoa brown; triangular or rounded occipital complex with underdeveloped lambdoidal crests; a low sagittal crest; and elongate upper incisors with parallel tips (Eger, 2008; Loureiro et al., 2018a). Descriptions and measurements of *Molossus molossus* were provided by Husson (1962, 1978), Dolan (1989), Ascorra et al. (1993), Simmons and Voss (1998), Barquez et al. (1999), Reid (2009), Lim and Engstrom (2001b), Lim et al. (2005), Barros (2014), Catzeflis et al. (2016), Giménez and Giannini (2016), and Loureiro et al. (2018a, 2018b). As noted above, multiple subspecies were traditionally recognized in *M. molossus* (e.g., by Simmons, 2005; Eger, 2008), but several have now been removed to other taxa (Loureiro et al., 2019). There is current disagreement concerning trinomial usage for the populations that occur east of the Andes in Peru: Simmons (2005) indicated that these should be called *M. m. molossus*, whereas Eger (2008) placed them in *M. m. crassicaudatus*. Although recent molecular studies support Simmons' nomenclature (Lindsey and Ammerman, 2016; Loureiro et al., 2018b, 2019), a comprehensive review of the species is needed, preferably based on analyses that include sequence data from holotypes or topotypic specimens of all nominal taxa currently treated as synonyms or subspecies.

Ascorra et al. (1993), Fleck et al. (2002), and Medina et al. (2015) correctly identified their specimens from Jenaro Herrera, Nuevo San Juan, Quebrada Sábalo, and Río Blanco as *Molossus molossus*. Most of the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions and measurements of the nominotypical subspecies, but one of our vouchers (AMNH 278458) is an albino (Tello et al., 2014).

Remarks: Of 192 recorded captures of *Molossus molossus* accompanied by ecological data from our region, 83 were made in ground-level mistnets and 109 in elevated nets. Most (187) of these mistnet captures were made in clearings around buildings, but 2 were captured over a stream and 3 were captured above secondary vegetation. Both of the roosts we encountered were in buildings. Vast numbers (perhaps hundreds) of these bats sheltered between the ceiling and the roof of the school at Nuevo San Juan, and most (if not all) of the 35 individuals that we mistnetted there on 21 June 1998 had probably just emerged from the schoolhouse (our nets were set between the school and the river at dusk in anticipation of the event). At El Chino, we captured two individuals from a larger group that was roosting in a crack between the rafters and the roof of the village school, and it is likely that most of the 139 individuals mistnetted in clearings at Jenaro Herrera had emerged from roosts in nearby station buildings that they are known to inhabit (Ascorra et al., 1993).

Molossus rufus É. Geoffroy St.-Hilaire, 1805

Figure 37B

Voucher material (total = 13): Jenaro Herrera (MUSM 6973), Nuevo San Juan (AMNH 273084, 273091, 273114, 273121, 273168; MUSM 15235–15239), Quebrada Betilia (MUSA 15194), Quebrada Sábalo (MUSA 15231); see table 64 for measurements.

Unvouchered observations: Ten individuals of *Molossus rufus* were captured, and others were detected using acoustic methods, during the CEBIO bat course at Jenaro Herrera in 2012.

Identification: The larger species of *Molossus* were recently revised by Loureiro et al. (2020), who split the taxon previously recognized as *Molossus rufus* into three species: *M. rufus* sensu stricto, *M. nigricans*, and *M. fluminensis*. As restricted by Loureiro et al. (2020), *Molossus rufus* can be distinguished from congeneric species by its dark dorsal pelage (varying from dark brown to blackish); dorsal hairs unicolored or, when bicolored, with a pale basal band covering no more than ¼ of the total length of each hair; dorsal hairs reaching 4.0 mm; forearm length averaging 50.3 mm in males (47.7–55.2) and 50.0 mm in females (46.7–54.0); greatest length

TABLE 64

External and Craniodental Measurements (mm) and Weights (g) of *Molossus rufus* and *Promops centralis* from the Yavarí-Ucayali Interfluve

	M. rufus		*P. centralis*	
	Males[a]	Females[b]	MUSM 6974 ♂	MUSM 5604 ♀
W	42.8 (34.3–58.0) 7	36.1 (26.0–47.0) 4	20.0	25.0
ToL	146.6 (142–150) 7	138.8 (121–147) 4	133	130
LT	55.1 (51–60) 7	50.8 (45–54) 4	58	55
HF	15.7 (11–21) 7	15.0 (13–17) 4	10	10
E	19.9 (19–22) 7	18.8 (18–19) 4	17	15
F	53.6 (51.0–55.0) 7	52.5 (51.0–54.0) 4	51.7	49.6
GLS	22.3 (21.5–22.9) 4	(21.4) 1	19.9	19.3
CIL	21.1 (21.0–21.5) 3	20.3 (19.9–20.8) 2	19.2	18.6
PB	4.7 (4.5–4.8) 4	4.7 (4.5–4.9) 2	4.1	4.1
BB	11.3 (11.1–11.5) 4	(11.0) 1	10.3	10.2
MB	13.9 (13.1–14.3) 4	13.4 (12.8–14.1) 2	11.6	11.5
ZB	14.2 (13.8–14.7) 4	13.8 (13.7–13.9) 2	12.5	12.1
MTL	8.3 (8.1–8.5) 4	8.0 (8.0–8.1) 2	7.4	7.3
BAM	10.0 (10.0–10.1) 4	9.8 (9.7–10.0) 2	9.1	9.1

[a] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273084, 273091; MUSM 6973, 15235, 15236, 15238, 15239.

[b] Summary statistics (mean, observed range in parentheses, and sample size) for measurements of AMNH 273114, 273121, 273168; MUSM 15237.

of skull averaging 22.9 mm (20.8–23.8) in males and 21.3 mm (19.9–22.6) in females; skull with inflated rostrum and elongated braincase; mastoid process directed laterally in posterior view; well-developed sagittal crest, particularly in males; basioccipital pits moderately deep; rostrum triangular in frontal view; and pincerlike upper incisors with converging tips (Loureiro et al., 2020).

Descriptions and measurements of *Molossus rufus* (which in the older literature was sometimes referred to by its junior synonym, *M. ater*) were provided by Husson (1962, 1978), Dolan (1989), Barquez et al. (1999), Simmons and Voss (1998), Gregorin and Taddei (2000), Lim et al. (2005), Nogueira et al. (2008), Peters et al. (2012), Rengifo et al. (2014), Giménez and Giannini (2016), and Loureiro et al. (2018a, b, 2019, 2020). No subspecies are currently recognized (Loureiro et al., 2020).

Ascorra et al. (1993) identified the Jenaro Herrera specimen as *Molossus ater*, but they mistakenly reported its catalog number as MUSM 6974. Fleck et al. (2002) and Medina et al. (2015) correctly identified their specimens from Nuevo San Juan, Quebrada Betilia, and Quebrada Sábalo as *Molossus rufus*. Most of the voucher material we examined from the Yavarí-Ucayali interfluve conforms to previous descriptions and measurements of the species, but one specimen (MUSM 15235) has a supernumerary pair of lower incisors.

Remarks: Of 10 recorded nocturnal captures of *Molossus rufus* accompanied by ecological information from our region, two were made in ground-level mistnets and eight in elevated nets; one individual was captured in primary forest, but the rest were netted in clearings.

We found five roosts of *Molossus rufus* near Nuevo San Juan (table 65), all of them in cavities

TABLE 65

Roosting Groups of *Molossus rufus* Observed near Nuevo San Juan

Date	Roost site	Group size	Entire group captured?	Age and sex of captured specimens
11 Sep 1999	cavity in standing tree	8	no	2 ad. males
15 Sep 1999	cavity in standing tree	5	yes	5 ad. males
23 Sep 1999	cavity in standing tree	about 14	no	2 ad. males, 5 ad. females
28 Sep 1999	cavity in standing tree	"many"	no	4 ad. females
22 Oct 1999	cavity in standing tree	at least 17	no	3 ad. males, 12 ad. females

in standing trees at recorded heights of 9–25 m above the ground. Four were in small cavities that appeared to have originally been excavated by woodpeckers, but one roosting group was found in the large central cavity of a hollow tree. Two roosts were in trees on the banks of the Río Gálvez, and one was in seasonally flooded forest near an oxbow lake, but two others were in primary upland forest far from water. Two roosts were in the swollen part of the trunks of *Iriartea deltoidea* palms, another was in the trunk of an *Astrocaryum jauari* palm, and the other two were in the trunks of unidentified dicotyledonous trees. *Molossus rufus* was usually found roosting alone, but one roost was shared with *Noctilio albiventris* and another with *Phyllostomus hastatus* and *Carollia perspicillata*.

Most previously reported roosts of *Molossus rufus* have also been in cavities in standing trees (Goodwin and Greenhall, 1961; Handley, 1976; Patterson, 1992), which are evidently the preferred diurnal refugia of this species.

Promops centralis Thomas, 1915

Voucher material (total = 2): Jenaro Herrera (MUSM 5604, 6974); see table 64 for measurements.

Unvouchered observations: *Promops* cf. *centralis* was recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera in 2012.

Identification: *Promops* is a Neotropical genus of three currently recognized species that can be distinguished from other molossids by the following combination of traits: ears short, rounded, and arising medially from the same point on the forehead; antitragus pendant and constricted at its base; tragus minute; lips smooth; snout with a median ridge extending from behind the nares to the level of the ears; palate highly domed; basisphenoid pits well developed; upper incisors curved, relatively slender, and less than half the height of the canines; two pairs of lower incisors; and lower incisors weakly bifid with the outer incisors crowded laterally behind the inner incisors (Eger, 2008). Size is said to differentiate *Promops centralis* from *P. nasutus* (e.g., Eger, 2008; López-Baucells et al., 2018), but there is considerable measurement overlap between these species (e.g., in forearm length and greatest length of skull; Gregorin and Taddei, 2000; Gregorin and Chiquito, 2010). *Promops centralis* can be more confidently distinguished from other congeners by its blackish- to chocolate-brown or dark reddish-brown bicolored dorsal pelage (with a whitish basal band that is 20% of the total length of the hairs) and slightly paler ventral pelage (Gregorin and Chiquito, 2010). Descriptions and measurements of *Promops centralis* were provided by Goodwin and Greenhall (1961, 1962), Carter and Dolan (1978), Ascorra et al. (1993), Simmons and Voss (1998), Barquez et al. (1999), Gregorin and Taddei (2000), Reid (2009), Lim and Engstrom (2001b), Gregorin and Chiquito (2010), and Giménez and Giannini (2016). No subspecies are currently recognized, but a revision of the spe-

cies is needed (Eger, 2008; Gregorin and Chiquito, 2010).

Ascorra et al. (1993) identified the specimens from Jenaro Herrera as *Promops centralis*, but they mistakenly reported the catalog number of one specimen (MUSM 6974 as MUSM 6973). Their voucher material conforms to previous descriptions and measurements of the species.

Remarks: No ecological information is available for this species in our region.

MATSES NAMES FOR AND KNOWLEDGE OF BATS

As previously summarized by Fleck et al. (2002), the Matses appear to have only a single lexicalized term, kuesban, for all local species of bats, yet they recognize morphological and behavioral diversity among multiple unnamed types of bats that plausibly correspond to biological families, subfamilies, genera, and species. The existence of such a sublexical classification—i.e., a classification that exists below the level of a named terminal folk taxon—was a novel finding in the field of ethnobiology. A brief summary of the results that supported this conclusion is provided in the following paragraphs.

During the initial interviews (conducted in 1994), Matses hunters were asked to list the different types of bats that they knew. The five interviewees responded with a mean of 16.6 responses (range: 8–22), totaling 83 cumulative responses distributed among 43 different bat descriptive terms. Descriptive terms elicited in these exercises referred either to appearance (e.g., "reddish bat"), roosting habits (e.g., "bat that is in hollow termite nests"), diet (e.g., "fish-eating bat"), or vocalization (e.g., "bat that says 'cosh'"). Clearly, the Matses observe variation in bat morphology and behavior, but such responses do not conclusively prove that they recognize different categories of bats. (There is always some variation among members of any category in the natural world, so the Matses could simply be describing differences among bats in the same way they recognize and describe morphological or behavioral variation among, say, domestic dogs.) Additionally, it was not clear whether such responses were actual folk-taxon names (lexemes) or simply ad hoc descriptive phrases.

The elicitation of bat names using specimens revealed a high degree of inconsistency among informants, suggesting that their responses were ad hoc descriptive phrases rather than lexemes, which one would expect to be more consistently used. For example, respondents presented with mistnetted specimens of *Peropteryx pallidoptera* variously named them as "little yellow bat," "little bat," "red bat," "little red bat," "little fleshy-nosed bat," and "long-nosed bat" (table 66). Significantly, all responses elicited in the village by dead specimens in 1998 described aspects of morphology, whereas responses elicited in the forest using bats shot at roosts in 1999 were descriptive of roosting behavior in addition to morphology. No responses elicited using dead bats in either circumstance mentioned feeding habits or vocalizations, suggesting that only directly observable characteristics were referenced.

Subsequent linguistic analyses consistently supported the conclusion that Matses responses to name elicitation were ad hoc descriptive phrases. All elicited responses consisted of the category name kuesban ("bat") modified by an enclitic, adjective, noun, or relative clause, and morpho-syntactic tests showed that additional words or morphemes could be inserted between the words and morphemes that made up elicited descriptive phrases (which would not have been possible with lexicalized terms).[13] Although it seems clear from these results, that the Matses have only one word for "bat," other evidence suggests that they really are aware of multiple unnamed categories of bats.

Analyses of monologs—a novel method for the study of folk classification at the time of our 2002 publication—provided the most compelling evidence for sublexical category recognition. The monolog elicitation method used in 1998 (when

[13] The essential logic of such morpho-syntactic tests is explained with English-language examples in Fleck et al. (2002).

TABLE 66

Results of Name Elicitation with Specimens of *Peropteryx pallidoptera*

Date	Voucher #	Informant[a]	Response	Translation
22 May 98	AMNH 272671	F	cuesban bëshpiumpi	"little yellow bat"
22 May 98	AMNH 272671	K	cuesbanëmpi	"little bat"
22 May 98	AMNH 272671	O*	cuesban piu	"red bat"
11 June 98	AMNH 272726	F	cuesban piumpi	"little red bat"
8 July 98	MUSM 13230	F	cuesban dëuishquedompi	"little fleshy-nosed bat"
8 July 98	MUSM 13230	F	cuesban dëuisac	"long-nosed bat"
4 Sep 99	AMNH 273042	F	cuesban dëuishquedo	"fleshy-nosed bat"
4 Sep 99	AMNH 273042	Q*	cuesban dëpuen shëcuën icquid	"bat that is in gully holes"
16 Sep 99	MUSM 15249	P*	cuesban piu	"red bat"
22 Sep 99	MUSM 15250	F*	dëpuen shëcuën diadquid cuesban	"bat that hangs in gully holes"
23 Sep 99	AMNH 273116	F*	cuesban dëuishquedo	"fleshy-nosed bat"
11 Oct 99	MUSM 15252	F*	cuesban acte cuitsipanën icquid	"bat that is in stream banks"
11 Oct 99	MUSM 15252	F*	cuesban dëuishquedo	"fleshy-nosed bat"
27 Oct 99	AMNH 273185	G*	cuesban dëuishquedo	"fleshy-nosed bat"

[a] Asterisks indicate informants who had seen roosts.

there was no further prompting and no prior discussion; see Materials and Methods) was essential for supporting our claim that the Matses recognize multiple types of bats, because the Matses spontaneously stated that there were multiple types. Thus, a 40-year-old man interviewed at Nuevo San Juan in 1998, remarked,

> Bats exist in different ways. Bats sleep under trees. Bats sleep in wild banana plants. Bats sleep in termite nests. Bats sleep under buttress roots. Bats hang on the trunks of very dry trees. Other bats are under big fallen trees, where the tree is twisted. Also, others are in big hollows, in big hollows of big tëmpa trees. There are very, very many kinds of bats.

Additionally, the 1998 interviews included several examples of kinds of bats characterized by multiple shared attributes, such as size and behavior (e.g., "One that is very small, that one lives on the river") or size and coloration ("There is another big bat, a very dark-colored one …").[14]

[14] Both quoted sentences are among the examples translated by Fleck et al., 2002: 84).

Such clustering of traits provides compelling evidence for the recognition of a natural category (i.e., a category where the members share multiple features), as opposed to simply recognizing variation within a category. For example, though there are no distinct breeds among Matses hunting dogs, the Matses recognize that there is much variation, even among littermates, most notably with respect to coloration, size, fur length, and propensity to become good hunting dogs, but they do not cluster these features into categories. In other words, they don't claim that black dogs are larger, or that short-haired dogs are better hunters.

Such trait clustering is even more prevalent in the 2010 monologs (translated in appendix 4), which were prompted by mentioning kinds of bats previously identified by the speaker (see Materials and Methods). These texts are also much longer than the 1998 monologs, and they contain far more substantive detail. Whereas the seven bat monologs recorded in 1998 ranged from 1:39 to 2:25 minutes, the two monologs recorded in 2010 lasted 20:23 minutes

(DWF1051c) and 9:22 minutes (DWF1055b). Although it is not particularly surprising that more information should be obtained by asking about each type of bat separately, these new recordings do suggest that Matses hunters know far more about bats than was apparent in 1998. However, at least some of this additional detail is clearly inaccurate.

Among other noteworthy inaccuracies and ambiguities, the narrator of DWF1051c states that the bats that enter houses to eat plantains (all of which are certainly phyllostomids) are the same ones that roost and raise their young in the roof thatch; the latter, however, are probably molossids or vespertilionids, the only Neotropical taxa definitely known to roost in thatch. Later, the same narrator asserts that the bats that roost in the rolled new leaves of wild monocots (clearly *Thyroptera tricolor*) are the same that eat figs and leave piles of fruit fragments under their feeding perches (which can only be stenodermatines). The same speaker also associates bats that roost in termite nests (usually *Lophostoma* spp., but possibly also *Phyllostomus hastatus*) with fig-eating bats, and he seems to confuse molossids (the only bats with free tails) with emballonurids (the only bats that routinely roost on exposed tree trunks. Lastly, he claims that female bats carry their older offspring on their backs, which no bat is known to do, and which is incompatible with flight. By contrast, the narrator of DWF1055b is more circumspect and does not impute feeding behavior to bats characterized by roosting traits, or vice versa.

DISCUSSION

The zoological information in this monograph is based on specimens obtained over many decades by dozens of people, some of whom were professional collectors rather than trained researchers. Supporting field notes are simply unavailable for many specimens, which are accompanied only by localities, dates, and external measurements recorded on labels. Additionally, few records exist of bats that were captured and released, such that the capture-frequency data at hand are limited to field notes from deliberately planned inventory research at just a few sites in our region. With such incomplete information, faunal analyses are necessarily limited and somewhat superficial. Below we discuss inventory completeness before briefly considering biogeographic and ecological topics.

Inventory Completeness

The capture records summarized in this report document the presence of 98 species of bats in the Yavarí-Ucayali interfluvial region. This result is not unexpected, because similar numbers of species have been reported or extrapolated from faunal inventory research at other Amazonian localities (Simmons and Voss, 1998; Lim and Engstrom, 2001a; Sampaio et al., 2003; Rex et al., 2008). However, despite the impressive effort and multiyear duration of faunal inventory work in our region (see Materials and Methods), we doubt that our inventory is complete. Several lines of evidence suggest that more species remain to be discovered.

The first indication that our inventory is incomplete is the large number of singletons in our material. In the context of biological inventory analysis (Colwell and Coddington, 1994; Coddington et al., 2009), singletons are species represented by unique observations: for example, single mistnet captures or captures at a single roost.[15] Of the 98 species positively recorded from the Yavarí-Ucayali interfluve, at least 11 are singletons (table 67). On the assumption that we are sampling from an underlying distribution of true detection probabilities (Chao et al., 2017), extrapolation sug-

[15] The essential concept here is independent sampling events, so a singleton taxon might be represented by multiple nonindependent captures. Although sampling independence is not without ambiguity in the present context, we counted each mistnet or harp-trap capture of a species as an independent event, even if multiple captures occurred at the same place on the same night; by contrast, we considered multiple conspecific captures at the same roost as one event even if they occurred on different dates.

TABLE 67

Bat Species Identified from Specimens Captured in the Yavari-Ucayali Interfluve

	Localities[a]				
	JH	NSJ	RT/QB	Other	Total records[b]
Cormura brevirostris	X	X		X	>10
Cyttarops alecto				X	1
Diclidurus isabella				X	1
Peropteryx kappleri	X	X			6
Peropteryx leucoptera		X	X		4
Peropteryx macrotis			X		1
Peropteryx pallidoptera		X	X	X	>10
Rhynchonycteris naso	X	X	X	X	>10
Saccopteryx bilineata	X	X	X	X	>10
Saccopteryx canescens				X	4?
Saccopteryx leptura	X	X		X	>10
Noctilio albiventris	X	X		X	5?
Noctilio leporinus				X	3?
Carollia benkeithi	X	X	X	X	>10
Carollia brevicauda	X	X	X	X	>10
Carollia perspicillata	X	X	X	X	>10
Desmodus rotundus	X		X	X	>10
Diphylla ecaudata				X	3
Anoura caudifer	X	X		X	4
Choeroniscus minor	X	X		X	5?
Glossophaga bakeri			X	X	10?
Glossophaga soricina	X	X	X	X	>10
Glyphonycteris daviesi		X			1
Glyphonycteris sylvestris		X			1
Trinycteris nicefori	X	X	X		9?
Hsunycteris dashe		X			2
Hsunycteris pattoni	X	X	X	X	>10
Hsunycteris thomasi	X		X	X	6?
Lionycteris spurrelli				X	1
Lampronycteris brachyotis		X			3
Micronycteris brosseti	X			X	2?
Micronycteris matses		X		X	6
Micronycteris megalotis	X	X	X	X	6?
Micronycteris microtis		X			>10
Micronycteris minuta		X		X	2
Micronycteris hirsuta	X	X			4

TABLE 67 *continued*

	Localities[a]				
	JH	NSJ	RT/QB	Other	Total records[b]
Chrotopterus auritus	X	X		X	3
Gardnerycteris crenulata	X	X	X	X	>10
Lophostoma brasiliense	X	X		X	4?
Lophostoma carrikeri	X			X	2
Lophostoma silvicolum	X	X	X	X	>10
Macrophyllum macrophyllum		X			1
Phylloderma stenops	X	X			3?
Phyllostomus discolor	X			X	6?
Phyllostomus elongatus	X	X	X	X	>10
Phyllostomus hastatus	X	X	X	X	>10
Tonatia maresi	X	X	X	X	10
Trachops cirrhosus	X	X	X	X	>10
Vampyrum spectrum	X				>1
Rhinophylla fischerae	X	X	X	X	>10
Rhinophylla pumilio	X	X	X	X	>10
Artibeus concolor	X				6?
Artibeus lituratus	X	X	X	X	>10
Artibeus obscurus	X	X	X	X	>10
Artibeus planirostris	X	X	X	X	>10
Artibeus anderseni	X	X	X	X	>10
Artibeus bogotensis	X				1
Artibeus cinereus				X	>10?
Artibeus glaucus	X	X	X	X	6?
Artibeus gnomus	X	X	X	X	>10
Chiroderma trinitatum	X			X	9?
Chiroderma villosum	X		X	X	>10
Enchisthenes hartii	X			X	4?
Mesophylla macconnelli	X	X		X	>10
Platyrrhinus angustirostris	X				2?
Platyrrhinus brachycephalus	X		X	X	>10
Platyrrhinus fusciventris	X				4?
Platyrrhinus incarum	X	X	X	X	>10?
Platyrrhinus infuscus		X			5
Sphaeronycteris toxophyllum				X	1
Sturnira giannae	X	X		X	7?
Sturnira magna	X	X		X	>10?
Sturnira tildae	X			X	>10

TABLE 67 *continued*

	Localities[a]				
	JH	NSJ	RT/QB	Other	Total records[b]
Uroderma bilobatum	X	X	X	X	>10
Uroderma magnirostrum	X		X	X	3?
Vampyressa thyone	X		X	X	>10
Vampyriscus bidens			X	X	3?
Vampyriscus brocki	X		X	X	>10
Vampyrodes caraccioli			X	X	3
Furipterus horrens	X	X		X	>10
Thyroptera discifera	X				1
Thyroptera lavali	X			X	5?
Thyroptera tricolor		X	X	X	>10
Thyroptera wynneae	X				1
Eptesicus brasiliensis	X	X		X	4?
Eptesicus furinalis	X		X		7
Lasiurus ega			X		5
Myotis albescens	X	X	X	X	>10?
Myotis nigricans	X		X		>10
Myotis riparius	X	X	X	X	>10?
Myotis simus				X	3?
Cynomops planirostris	X				5
Eumops hansae			X	X	3
Molossops neglectus	X				4?
Molossus coibensis	X				6?
Molossus molossus	X	X	X	X	>10
Molossus rufus	X	X		X	>10
Promops centralis	X				2?
TOTALS (number of species):	71	56	46	71	

[a] Abbreviations: JH, Jenaro Herrera; NSJ, Nuevo San Juan; RT/QB, Río Tahuayo/Quebrada Blanco (including El Chino Village, Frog Valley, Tahuayo Farm, and Quebrada Blanco). "Other" includes 24 additional localities listed in appendix 1.

[b] Independent sampling events: e.g., mistnet captures or roost discoveries (not necessarily specimens collected; see text).

gests that additional inventory effort in our region would result in more species. Although the data at hand are far from ideal for analysis, an educated guess about the number of species in the fauna that remain undetected can be based on nonparametric estimators previously used for this purpose by Simmons and Voss (1998). Among others, the Chao1 estimator (Colwell and Coddington, 1994; Chao et al., 2017) is based on the number of singletons, a, and doubletons (species independently observed twice), b. The latter are somewhat more problematic to identify in our results than singletons due to the lack of explicit capture information for some specimens, but from what we can reasonably infer there may be as few as four or as many as seven doubletons in our material (table 67). The number of unobserved species estimated by Chao's method is just $a^2/2b$, which gives about 15 species if $b = 4$ and about 9 species if $b = 7$. Therefore, the true (unobserved) number of species in our region might be in the range of 107 to 113.

The above exercise is based on too many assumptions (some of which are discussed by Colwell and Coddington, 1994) to be taken at face value, and confidence intervals around such extrapolations are typically wide. However, it is noteworthy that these point estimates (9–15 unobserved species in our region) agree rather well with a second line of evidence for inventory incompleteness. This consists of our list of species that we did not capture, but that have geographic ranges that adjoin or overlap the Yavarí-Ucayali interfluve. There are 18 such species (appendix 2), providing just enough candidate taxa to suggest that even the higher value estimated by Chao's method is not unreasonable.

A third indication of inventory incompleteness is the fact that additional species were still being discovered by recent fieldwork in our region, long after faunal-inventory efforts peaked between 1988 and 1999 (when intensive, multi-year surveys were carried out at Jenaro Herrera and Nuevo San Juan; see Materials and Methods). In the two decades that followed, no fewer than 13 additional species were discovered by various teams of researchers, including *Sphaeronycteris toxophyllum* in 2003; *Diclidurus isabella* in 2008; *Thyroptera wynneae*, *Eptesicus furinalis*, *Cynomops planirostris*, and *Molossus coibensis* in 2012; *Cyttarops alecto*, *Diphylla ecaudata*, *Vampyrodes caraccioli*, and *Eumops hansae* in 2013; *Lionycteris spurrelli* in 2014; and *Peropteryx macrotis* and *Lasiurus ega* in 2019. Such recent additions suggest that species accumulation in our region has not yet reached an asymptote.

Fourth, the notion that our inventory is incomplete is supported by the observation that most (13 out of 18) of the expected species listed in appendix 2 are aerial insectivores, an ecobehavioral category of bats that is notoriously difficult to capture in mistnets (Voss and Emmons, 1996; Simmons and Voss, 1998; Sampaio et al., 2003). Although fieldworkers at several localities in our region have used supplementary methods known to be effective at capturing some aerial-insectivorous taxa, such methods are unlikely to have exhaustively sampled this feeding guild. Harp traps, for example, were only used during the one-week 2019 Tahuayo expedition, whereas searching for roosts has largely been confined to the forest understory, precluding the discovery of aerial insectivores that roost in the canopy or subcanopy (which might include the majority of expected molossids).

Lastly, the existence of uncaptured species in our region is also suggested by the results of acoustic monitoring at Jenaro Herrera in 2012, which recorded echolocation calls that plausibly match the known vocalizations of unvouchered species (e.g., *Lasiurus blossevillii*, *Nyctinomops macrotis*) or that might correspond to the still-undocumented vocalizations of others (e.g., *Diclidurus albus*, *Eumops* spp.).

Although none of these indications of inventory incompleteness is persuasive by itself, taken together they seem compelling. Ninety-eight species is a lot of bats, but we are persuaded that there are still more in our region awaiting discovery. Therefore, subsequent discussions of

TABLE 68

Taxonomic Composition of the Yavarí-Ucayali Bat Fauna

(Table entries are numbers of species and percent of the total fauna)

	Observed	Expected[a]
Emballonuridae	11 (11%)	13 (11%)
Noctilionidae	2 (2%)	2 (2%)
Phyllostomidae	66 (67%)	72 (62%)
Furipteridae	1 (1%)	1 (1%)
Thyropteridae	4 (4%)	4 (3%)
Vespertilionidae	7 (7%)	8 (7%)
Molossidae	7 (7%)	17 (15%)
TOTALS:	98	116

[a] Observed species plus those expected based on geographic-range overlap (appendix 2).

taxonomic composition, biogeography, and trophic structure must take inventory incompleteness into consideration.

Taxonomic Composition and Biogeography

The higher-level taxonomic composition of the Yavarí-Ucayali bat fauna (table 68) is typical of bat faunas throughout the humid Neotropical lowlands with only a few exceptions. As usual, Phyllostomidae is by far the most diverse family, comprising well over half of the species in our region. All the remaining families are also ubiquitous—if much less diverse—elements of Neotropical rainforest bat faunas as previously indicated by inventory results from widely scattered localities (e.g., Simmons and Voss, 1998; Lim and Engstrom, 2001a, b; Sampaio et al., 2003; Hice et al., 2004), but the absence of mormoopids and natalids is noteworthy. Mormoopids and natalids are typically cave-roosting taxa (Gardner, 2008c), and their absence might be explained by the lack of rock outcrops in our region (except in the still-poorly sampled Sierra del Divisor). However, some mormoopids are known to occur at caveless localities (Simmons and Voss, 1998; Sampaio et al., 2003), so the absence of this family throughout much of western Amazonia is hard to understand. Thyropterids are notably more diverse in our region than elsewhere in the Neotropics (Velazco et al., 2014), another faunal peculiarity that resists easy explanation. Differences in higher-taxonomic composition between observed and expected faunas are small except for Molossidae, which future collecting might show to be much more speciose than our present results indicate.

Many Neotropical rainforest bat species are widespread, with geographic ranges that span multiple biomes separated by high elevations in the Andes or broad expanses of nonforest vegetation (fig. 38). At least 79 species of the Yavarí-Ucayali interfluvial fauna are widespread in this sense, including 44 species that occur in all four lowland rainforest biomes (trans-Andean, coastal Venezuelan, Amazonian, and Atlantic) and another 35 that occur in two or three biomes; only 19 species in our fauna have predominantly Amazonian distributions (table 69). Many species in the latter category are not strictly confined to Amazonia, because some of them also occur in gallery forests that extend into adjacent nonforest biomes (e.g., the Llanos and Cerrado), others range into premontane or lower-montane habitats in the Andes, and several extend southward along the base of the Andes into semideciduous foothill formations in Bolivia. Nevertheless, this is the most biogeo-

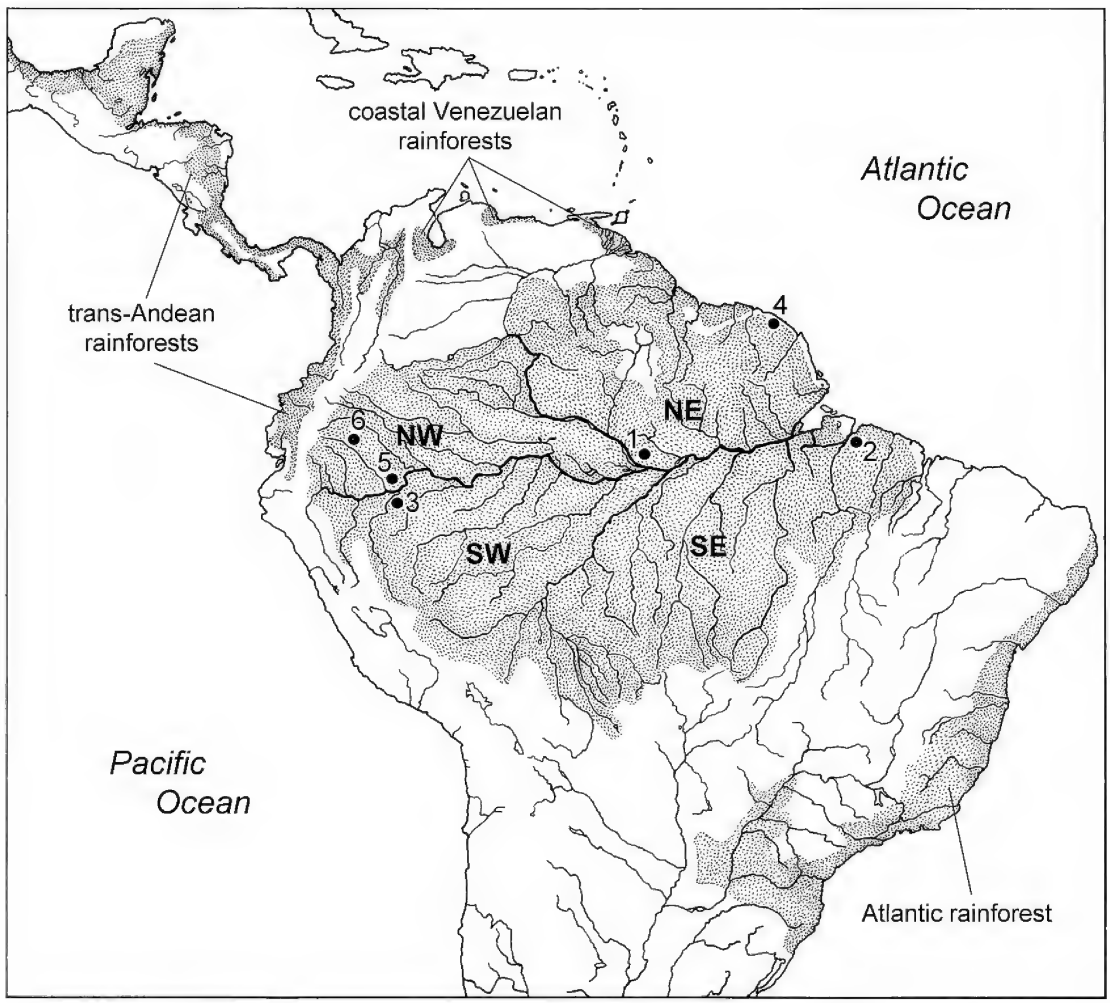


FIG. 38. Four Neotropical lowland rainforest biomes (stippled) separated by montane or nonforest vegetation. Primary intercardinal directions (NE, NW, SE, SW) label quadrants of Amazonia defined by the Amazon, Madeira, and Negro rivers (after Wallace, 1852). Six Amazonian bat inventory sites mentioned in the text are: **1,** BDFFP (= Biological Dynamics of Forest Fragments Project; Amazonas, Brazil); **2,** Belém (Pará, Brazil); **3,** Jenaro Herrera (Loreto, Peru); **4,** Paracou (French Guiana); **5,** RNAM (= Reserva Nacional Allpahuayo-Mishana; Loreto, Peru); and **6,** Tiputini (Orellana, Ecuador).

graphically distinctive component of our fauna, and for lack of a better term we will refer to such species as Amazonian endemics.

Most (58%) of these endemics occur in all four Amazonian quadrants traditionally delimited by major rivers (the upper and lower Amazon, the Rio Negro, and the Rio Madeira; table 70), and one species (*Peropteryx pallidoptera*) appears to be absent only in southeastern Amazonia. Three species (*Glossophaga bakeri*, *Platyrrhinus infuscus*, and *Sturnira magna*) seem to be western Amazonian taxa; one (*Carollia benkeithi*) is southern Amazonian; and one (*Micronycteris brosseti*) is, somewhat improbably, known from northeastern and southwestern Amazonia. Only two local species (*Micronycteris matses*, *Hsunycteris dashe*), both recently described from material collected at Nuevo San Juan, are known only from southwestern Amazonia.

TABLE 69

Summary of Distributional Patterns of Bat Species from the Yavarí-Ucayali Interfluve

Distribution[a]	Species
All four rainforest biomes	43
All but Atlantic Forest	10
All but Trans-Andean forests	6
All but coastal Venezuelan forests	5
Amazonia plus Atlantic Forest	8
Amazonia plus Trans-Andean forests	3
Amazonia plus coastal Venezuelan forests	4
Amazonia only	19

[a] Documented occurrence in Neotropical rainforest biomes (fig. 38) as summarized in appendix 3.

In effect, most of the observed bat fauna of the Yavari-Ucayali interfluve consists of geographically widespread taxa. Very few species in our region are narrowly endemic, in keeping with the low endemicity reported from previous analyses of Amazonian bat faunas (Voss and Emmons, 1996; Simmons and Voss, 1998) and the general lack of evidence that even the largest rivers are dispersal barriers for bats. The additional species that might be expected to occur in our region are also widespread taxa (appendix 2), so future collecting seems likely to further dilute the endemic component of the local fauna unless there are large numbers of elusive new species that remain to be discovered. Although we cannot discount that possibility, it does not seem very realistic.

Community Composition and Trophic Structure

Only subsets of the 98 species captured in the Yavarí-Ucayali interfluve are known to occur at even the best-sampled localities in our region; for example, just 71 species are documented by specimens captured at Jenaro Herrera (table 67). This disparity, and the even wider disparities between observed species richness at single localities and expected numbers of species in the regional fauna (107–113 species based on extrapolation, 116 species based on geographic-range overlap; see above) might have two nonexclusive explanations. Either local communities in our region have been incompletely inventoried, or some species in the regional fauna do not occur in local faunas due to some sort of ecological filtering.

Incomplete sampling is a plausible explanation for the absence of many regional species in local communities because no locality in our region has been sampled intensively using all essential inventory methods. Essential inventory methods include ground-level mistnetting, elevated ("canopy") mistnetting, and searching for roosts, each of which effectively samples only a subset of Neotropical rainforest bat faunas (Voss and Emmons, 1996; Simmons and Voss, 1998; Kalko and Handley, 2001). No elevated mistnetting was accomplished at Nuevo San Juan, for example, and ground-level mistnetting there was only carried out for a few weeks in the dry season of 1998. By contrast, although intensive ground-level and elevated mistnetting was carried out over multiple seasons and years at Jenaro Herrera, searching for roosts at Jenaro Herrera was sporadic and haphazard. All the other sites in our region received far less inventory effort, and their known faunas are correspondingly depauperate.

Making a compelling case for ecological filtering is difficult, but widespread species of cave-roosting bats (e.g., *Lonchorhina* spp.) seem unlikely to occur in the absence of rock outcrops, which are entirely lacking throughout most of our region. Another possibility is that some bats only inhabit seasonally flooded forests or other riparian vegetation that is absent at upland sites. Some species that might be riparian-habitat specialists (e.g., *Glossophaga bakeri*, *Myotis simus*) are only known from our region at riverside localities (e.g., Isla Muyuy, Orosa, and El Chino Village), so ecological filtering might explain their absence at Jenaro Herrera, which is several kilometers inland from the Río Ucayali and occupies a terrace above the river floodplain. In the absence of definite knowledge about relevant autecologies, however, this is mere conjecture.

TABLE 70

Distributions of 19 Amazonian Endemics Present in the Yavarí-Ucayali Interfluve

Species	Distribution[a]	References
Peropteryx pallidoptera	NE, NW, SW	Castro et al. (2012)
Carollia benkeithi	SE, SW	McLellan and Koopman (2008)
Glossophaga bakeri	NW, SW	Griffiths and Gardner (2008a)[b]
Hsunycteris dashe	SW	Velazco et al. (2017)
Hsunycteris pattoni	NE, NW, SE, SW	Mantilla-Meluk et al. (2010), Velazco et al. (2017)
Micronycteris brosseti	NE, SW	Williams and Genoways (2008), this report
Micronycteris matses	SW	Simmons et al. (2002), Medina et al. (2015)
Lophostoma carrikeri	NE, NW, SE, SW	Brandão et al. (2020)
Rhinophylla fischerae	NE, NW, SE, SW	McLellan and Koopman (2008)
Artibeus concolor	NE, NW, SE, SW	Marques-Aguiar (2008a)
Platyrrhinus brachycephalus	NE, NW, SE, SW	Velazco (2005)
Platyrrhinus fusciventris	NE, NW, SE, SW	Velazco et al. (2010a)
Platyrrhinus infuscus	NW, SW	Velazco (2005)
Sturnira giannae	NE, NW, SE, SW	Velazco and Patterson (2019)
Sturnira magna	NW, SW	Gardner (2008h)
Vampyriscus bidens	NE, NW, SE, SW	Arroyo-Cabrales (2008c)
Vampyriscus brocki	NE, NW, SE, SW	Arroyo-Cabrales (2008c)
Thyroptera lavali	NE, NW, SE, SW	Wilson (2008a), García et al. (2019)
Myotis simus	NE, NW, SE, SW	Moratelli et al. (2015b)

[a] Documented occurrence in Amazonian quadrants delimited by major rivers (figure 38).
[b] But see this report for corrected identification of USNM 565513 from Guyana, erroneously mapped as *Glossophaga commissarisi* by Griffiths and Gardner (2008a: map 117).

Therefore, the data compiled for this report provide an unsatisfactory basis for ecological inference, but they are all we have. Based on the preceding remarks about inventory completeness, it seems likely that the observed bat faunas at localities in our region are methodologically biased subsets of local communities. However, if local communities are assembled from regional source faunas by ecological filtering, it seems improbable that all geographically expected species interact sympatrically. In the absence of relevant information about mechanisms of ecological filtering, the best we can do is to summarize trophic structure based on lists of locally observed species on the one hand and those that might be expected based on geographic-range overlap on the other. Because local communities are unlikely to be much smaller than observed faunas (which might include a few vagrants) or much larger than geographically expected faunas (which might lack a few species), these lists probably bracket the range of ecological possibilities.

The results of this exercise for Jenaro Herrera (table 71) suggest that frugivores outnumber other feeding guilds in the observed fauna, but not in the expected fauna, in which aerial insectivores predominate. If guilds are summed according to whether species are primary or secondary consumers, then primary consumers (frugivores and nectarivores; $N = 33$) are about as numerous as secondary consumers (aerial insectivores, gleaning insectivores, carnivores, piscivores, and san-

TABLE 71

Trophic Structure of Rainforest Bat Faunas in Western and Eastern Amazonia

(Table entries are numbers of species.)

	Jenaro Herrera[a]		Paracou[b]	
	Observed	Expected	Observed	Expected
Aerial insectivores[c]	20	43	28	47
Gleaning insectivores[d]	10	17	18	19
Carnivores[e]	3	3	3	3
Piscivores[f]	0	1	1	1
Sanguivores[g]	1	3	2	2
Frugivores[h]	28	33	18	22
Nectarivores[i]	5	10	5	7
Omnivores[j]	4	4	4	4
TOTALS	71	115	79	105

[a] In western Amazonia. Observed species are those listed from Jenaro Herrera in table 67. "Expected" species include observed species, 27 other species documented by captured specimens from elsewhere in the Yavarí-Ucayali interfluve (table 67), plus 16 of the 18 species listed in appendix 2 (excluding cave-roosting *Lonchorhina aurita* and *L. inusitata*).

[b] In eastern Amazonia. Observed species are those documented from Paracou voucher material (Simmons and Voss, 1998: table 69) minus *Micronycteris homezi* (now synonymized with *M. minuta*; Ochoa and Sánchez, 2005) plus one additional species each of *Pteronotus* (Pavan et al., 2018) and *Platyrrhinus* (Velazco et al., 2010). The "expected" fauna at this site includes observed species, 25 other species previously known from French Guiana or Surinam (Simmons and Voss, 1998: appendix 1), and *Diclidurus ingens* (recently reported from French Guiana; Catzeflis et al., 2013); however, we omit three stenodermatine species erroneously reported from French Guiana based on misidentifications (*Platyrrhinus lineatus*, *Vampyressa melissa*, *V. pusilla*), and we exclude nine other cave-roosting or savanna-associated species that seem unlikely to occur locally in the absence of rock outcrops and open areas (*Pteronotus gymnonotus*, *Pt. personatus*, *Choeroniscus godmani*, *Lonchorhina aurita*, *L. fernandezi*, *Phyllostomus latifolius*, *Platyrrhinus aurarius*, *Natalus tumidirostris*, *Rhogeessa hussoni*).

[c] Emballonurids, mormoopids, *Furipterus horrens*, *Thyroptera* spp., vespertilionids, and molossids.

[d] *Noctilio albiventris*, glyphonycterines, micronycterines, *Gardnerycteris crenulata*, *Lophostoma* spp., *Macrophyllum macrophyllum*, *Mimon bennettii*, *Tonatia* spp.

[e] *Chrotopterus auritus*, *Trachops cirrhosus*, *Vampyrum spectrum*.

[f] *Noctilio leporinus*.

[g] Desmodontines.

[h] *Carollia* spp., *Rhinophylla* spp., stenodermatines.

[i] Glossophagines and lonchophyllines.

[j] *Phylloderma stenops* and *Phyllostomus* spp.

guivores; $N = 34$) in the observed fauna. In the expected fauna, however, primary consumers ($N = 44$) are greatly outnumbered by secondary consumers ($N = 67$). Inferences about the abundance of individuals (or biomass) in these trophic categories are, of course, impossible due to the well-documented biases associated with mistnet capture data (Remsen and Good, 1996; Simmons and Voss, 1998).

Comparisons between the observed bat fauna at Jenaro Herrera with the observed fauna at Paracou, a well-sampled rainforest locality in eastern Amazonia (fig. 38, table 71) suggest several differences in trophic structure; for example, Jenaro Herrera has 44% fewer gleaning insectivores but 56% more frugivores than Paracou. Comparisons of the expected faunas at these localities, however, suggest approximate parity in most trophic categories, with the notable exception of frugivores, for which the surplus at Jenaro Herrera is about the same (55%). The numerical differences in aerial insectivores

TABLE 72

Numbers of Frugivorous Bat Species at Six Amazonian Inventory Sites

	Frugivores	Reference
Eastern Amazonia		
Belém, Brazil	20	Kalko and Handley (2001)
BDFFP[a], Brazil	19	Sampaio et al. (2003)
Paracou, French Guiana	18	Simmons and Voss (1998)
Western Amazonia		
Jenaro Herrera, Peru	28	This report
RNAM[b], Peru	29	Hice et al. (2004)
Tiputini, Ecuador	27	Rex et al. (2008)

[a] Biological Dynamics of Forest Fragments Project (80 km N Manaus).
[b] Reserva Nacional Allpahuayo-Mishana (25 km SW Iquitos).

and gleaning insectivores between the observed faunas at these localities can plausibly be attributed to methodological bias because both guilds were probably undersampled at Jenaro Herrera, but it is harder to explain away the differences in frugivore species richness. Unlike insectivorous bats, frugivorous species are readily captured in mistnets, which were used intensively at both sites at ground level and in the canopy. Does the difference in frugivore species richness between Jenaro Herrera and Paracou represent a real trophic difference between western and eastern Amazonian bat faunas, or is this difference site specific?

Inventory results from several other localities where bat communities have been sampled intensively by multiyear programs of ground-level and canopy mistnetting suggests that, in fact, western Amazonian bat faunas are richer in frugivorous species than eastern Amazonian faunas (table 72). The average difference (about 9 species) represents a 47% average increase in frugivorous species from east to west or, equivalently, a 32% average decrease from west to east; from either perspective, the difference is substantial. Although ecological explanations are outside the scope of this report, we note that an east-to-west increase in numbers of frugivorous bat species is consistent with the longitudinal gradient in Amazonian primary-consumer diversity previously hypothesized by Voss et al. (2001: 207–210), who discussed possible causes.

Matses Knowledge and Linguistic Recognition of Bat Diversity

The Matses encounter bats on a daily basis in a variety of circumstances. Many species roost near ground level in understory foliage or termite nests haphazardly encountered by men, women, and children; others occupy burrows that hunters routinely inspect for spoor of edible rodents and armadillos; and a small gray species perches in plain sight on trunks and snags at the river's edge. When men cut new garden plots from the forest, bats often emerge from cavities in felled trees. Insectivorous bats dart and swoop over clearings in the early evening, fishing bats zoom past canoe travelers on the river at dusk, and the crowns of fruiting trees are noisy with flapping wings at night. Some species enter Matses houses to eat stored fruit, and others drink blood from people, pets, and livestock. In the early morning, sleepers are often awakened by the noisy movements and vocalizations of bats returning to their diurnal refugia in the roof thatch overhead.

Broadly speaking, the Matses are familiar with just two aspects of bat behavior—feeding and roosting—but they seldom have the opportunity to

examine bats up close, so the morphological traits by which species might be accurately distinguished to link feeding behavior with roosting behavior are inapparent. Therefore, most of the obvious errors associated with our elicited monologs involve mismatches between observations about feeding behavior and roosting behavior—for example, between roosting in rolled new leaves and fig-eating or house-visiting—and such errors occurred both in the monologs recorded in 1998 and those recorded in 2010 using different elicitation protocols. Other errors, such as the repeated statements that bats first carry their young on their abdomens but later carry them on their backs, are perhaps extrapolations from the more familiar behavior of other mammals (such as opossums). Clearly, however, the Matses are less than astute observers of bat behavior, especially by comparison with the highly accurate ethnobiological information previously extracted from their monologs about primates and other game species (Fleck and Voss, 2016; Voss and Fleck, 2011, 2017).

Another aspect of our recorded texts is taxonomic ambiguity. With just a few exceptions—species with unique behaviors such as *Rhynchonycteris naso*, *Noctilio leporinus*, *Desmodus rotundus*, and *Thyroptera tricolor*—it is seldom possible to positively identify the bats described in Matses monologs. Although Matses descriptive phrases can sometimes be associated plausibly with higher taxa (genera, subfamilies, or families; Fleck et al., 2002), associations based on single attributes (e.g., "fleshy-nosed bats," "free-tailed bat") are seldom convincing in the absence of other context, which is lacking more often than not. The problem here is the absence of lexemic labelling (all bats are kuesban) by contrast with the elaborate Matses folk taxonomy previously documented for most of the larger fauna (Fleck and Voss, 2006; Voss and Fleck, 2011, 2017).

Linguistic underdifferentiation (i.e., referring to multiple biological species by a single folk-taxonomic lexeme) and ambiguous or erroneous natural-history observations are joint aspects of Matses inattention to small, nocturnal species that are culturally unimportant (Voss et al., 2019). As extensively analyzed and discussed by Fleck et al. (2002), the Matses are clearly aware that there are many local species of bats, but they seldom need to talk about them; therefore, there is no societal motivation for lexemic labeling. Although the disparity between exuberant chiropteran diversity (as documented in this monograph) and the poverty of the Matses lexicon for bats seems remarkable, the situation is not much different from that in Western cultures with languages (like English, French, German, Spanish, etc.) that similarly have only a single vernacular lexeme for bats.

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FIG. 39. A Matses boy delivers a leaf-package of live bats to our house in Nuevo San Juan in 1998 (photo by R.S.V.)

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APPENDIX 1

Gazetteer

Below we list the principal localities from which bats have been collected or observed in the Ucayali-Yavarí interfluvial region. Boldface identifies locality names as they appear in the text (alternative names or spellings are cited parenthetically). All localities are mapped in figure 2.

Amelia (4°20′S, 70°12′W; GeoNames, 2019): village at the edge of a rubber forest on the Río Yavarí some 20 miles above its mouth and opposite the Brazilian village of Remate de Males; visited by M.P. Anderson and W.H. Osgood. Osgood (1914) referred to this village as "Nazareth" and said they visited this site on 10 September 1912, but the date on bat specimen labels from Nazareth is 19 August 1912.

Anguila (6°16′S, 73°55′W; Pitman et al., 2015): inventory site in the headwaters of the Quebrada Yanayacu, a minor right-bank affluent of the Río Tapiche; surveyed for bats and other mammals by M. Escobedo-Torres from 14 to 20 October 2014 (Pitman et al., 2015). According to Pitman et al. (2015), this upland site included both tall forest (on hilly terrain and terraces) and stunted white-sand forest (*varillal*).

Divisor (7°12′S, 73°53′W; Vriesendorp et al., 2006): inventory site near Tapiche (q.v.) east of upper Río Tapiche in Sierra del Divisor (250–600 m); surveyed for bats and other mammals by M.L.S.P. Jorge and P.M.V. from 19 to 23 August 2005 (Jorge and Velazco, 2006). According to Vriesendorp et al. (2006), this site in the heart of the Sierra del Divisor consisted of steep ridges, hill slopes, and broad valley bottoms with a diversity of pristine upland forest formations.

El Chino Village (4°18′S, 73°13′W): inventory site on the right bank of the Río Tahauyo just below its confluence with the Quebrada Blanco (q.v.); surveyed for bats on several nights from 16 to 22 February 2019. See Materials and Methods for a description of habitats and fieldwork this site.

Estación Biológica Madre Selva (3°37′S, 72°14′W; Angulo and Díaz, 2004): research station on the south bank of the Río Orosa; surveyed for bats by J. Rios from 11–14 November 2003. The station's website (at www.projectamazonas.org; accessed in December 2020) suggests that a wide range of habitats (including upland forest, *várzea*, secondary vegetation, and swamps) are present at this locality, but no information is available about which were sampled for bats.

Frog Valley (4°21′S, 73°11′W): inventory site in well-drained upland forest on the right bank of the Quebrada Blanco (q.v.); surveyed for bats on 16–22 February 2019. See Materials and Methods for more information about fieldwork at this site.

Isla Muyuy (3°55′S, 73°14′W; GeoNames, 2019): an island 10 km long and 5 km wide, located in the Amazon, about 20 km southeast of Iquitos; surveyed for bats from August to September 1992 (Wilson et al., 1996). This "island" is separated from the right bank of the Amazon only during high water, when oxbow lakes on the island become connected to the river. Bat netting here was in primary forest, agricultural clearings, and secondary vegetation adjacent to flooded habitats.

Isla Padre (also known as "Padre Isla"; 3°39′S, 73°09′W; GeoNames, 2019): an 8 km^2 island located opposite the city of Iquitos on the right ("south") bank of the Amazon; surveyed for bats from 19 November to 10 December 1984 by V. Pacheco.

Jenaro Herrera (sometimes misspelled "Genaro Herrera" or "Henaro Errera"; 4°55′S, 73°40′W): botanical field station ca. 2.5 km inland from right bank of Río Ucayali; surveyed for bats by Ascorra et al. (1993), by the 2012 CEBIO field course students and faculty (16–24 January 2012), and by post-

course researchers (L. Arcila-Hernandez, W. Calderón, B.K. Lim, P.M.V., and R.S.V.; 22–29 January 2012).

Lago Preto (4°30′S, 71°43′W; Escobedo and Velazco, 2012): lake on left bank of the Río Yavarí, surveyed for bats by M. Escobedo-Torres on 29 May 2007. The predominant local natural habitat is early-successional riparian forest with clay soils and an open understory characterized by the presence of *Cecropia* sp., *Helicona* sp., and *Piper* sp.

Nuevo San Juan (5°15′S, 73°10′W; Fleck et al., 2002): inventory site on right bank of Río Gálvez; intensively sampled for mammals from 1995 to 1999 by D.W.F., and from 19 May to 12 July 1998 by R.S.V. See text for an account of habitats sampled for bats at this locality.

Orosa (ca. 3°32′S, 72°11′W; Wiley, 2010): collecting locality on the right (south) bank of the Amazon, where Alfonso and Ramón Olalla worked from 30 August to 11 December 1926 (probably near the modern village of San José de Orosa with above coordinates; Wiley, 2010). Hershkovitz (1977: 928) placed this locality on the Río Marañón, but Orosa lies well below the confluence of the Marañón and the Ucayali, so it is unambiguously on the Amazon (see Faura-Gaig [1964] for Peruvian fluvial nomenclature. According to Wiley (2010), much of the habitat here is seasonally inundated (*várzea*) forest.

Quebrada Betilia (headwater at 6°26′S, 73°24′W; Medina et al., 2015): tributary of the Río Yaquerana located in the northeastern section of the Zona Reservada Sierra del Divisor; this remote, upland site on upland hilly terrain was surveyed for bats and other mammals in the wet season of 2013 by Medina et al. (2015).

Quebrada Blanco (also known as "Río Blanco"; mouth at ca. 4°19′S, 73°14′W; Valqui, 2001): right-bank tributary of Río Tahuayo and site of extensive mammalogical research (e.g., by Heymann, 1989, 1990; Heymann and Aquino, 1994; Valqui, 2001; Heymann et al., 2011). The Estación Biológica Quebrada Blanco (EBQB; 4°21′S, 73°09′W; Heymann et al., 2011) was surveyed for bats by C. Ascorra from 23 October to 4 November 1992. Another locality that C. Ascorra surveyed for bats on the Quebrada Blanco was Comunidad de Limón (5–7 November 1992); although its coordinates are unknown, we assume that it was close to the EBQB, where Ascorra had collected just the day before. The Quebrada Blanco is not to be confused with the Río Blanco (q.v.), a tributary of the Río Tapiche.

Quebrada Buenavista (4°50′S, 72°23′W; Pitman et al., 2003): tributary of the Río Yavarí, roughly 65 km down the Yavarí from Angamos; a variety of forest types was present at this inventory site on a bluff above the Río Yavarí, but it is not known which local habitats were surveyed for bats (Escobedo, 2003).

Quebrada Curacinha (5°03′S, 72°44′W; Pitman et al., 2003): tributary of the Río Yavarí, roughly 20 km down the Yavarí from Angamos; surveyed for bats by M. Escobedo (Escobedo, 2003).

Quebrada Esperanza (ca. 4°20′S, 71°55′S; Stephens and Traylor, 1983): collecting locality of C. Kalinowski on the left bank of the Río Yavarí-Mirím (mouth at 4°31′S, 71°44′W), 6–27 September 1957.

Quebrada Limera (4°31′S, 71°54′W; Pitman et al., 2003): tributary of the Río Yavarí, roughly 130 km down the Yavarí from Angamos; surveyed for bats by M. Escobedo (Escobedo, 2003).

Quebrada Lobo (headwater at 6°30′S, 73°37′W; Medina et al., 2015): tributary of the Río Blanco located in the northeastern section of the Zona Reservada Sierra del Divisor; surveyed for bats and other mammals in the wet season of 2013 by Medina et al. (2015).

Quebrada Pantaleón (headwater at 6°25′S, 73°32′W; Medina et al., 2015): tributary of the Río Blanco, located in the northeastern

section of the Zona Reservada Sierra del Divisor; surveyed for bats and other mammals in the wet season of 2013 by Medina et al. (2015).

Quebrada Pobreza (5°59′S, 73°46′W; Pitman et al., 2015): inventory site on the eponymous stream, a left-bank affluent of the Río Blanco; surveyed for bats and other mammals by M. Escobedo-Torres, 20–26 October 2014 (Pitman et al., 2015).

Quebrada Sábalo (headwater at 6°22′S, 73°28′W; Medina et al., 2015): tributary of the Río Yaquerana located in the northeastern section of the Zona Reservada Sierra del Divisor; surveyed for bats and other mammals in the wet season of 2013 by Medina et al. (2015).

Quebrada Vainilla (3°32′S, 72°44′W; Robbins et al., 1991): collecting locality on the right (east) bank of Quebrada Vainilla, a minor right-bank tributary of the Amazon below Iquitos; surveyed for bats and birds by A.P. Caparella, S.W. Cardiff, T.J. Davis, D.L. Dittmann, T.C. Maxwell, M. Sánchez S, and A. Urbay T. from 13 July to 11 August 1983 (Robbins et al., 1991).

Río Blanco (6°24′S, 73°43′W; Medina et al., 2015): a right-bank tributary of the Río Tapiche; surveyed for bats and other mammals in the wet season of 2013 by Medina et al. (2015). Not to be confused with the Quebrada Blanco (q.v.), a tributary of the Río Tahuayo.

San Fernando (4°12′S, 70°14′W; Stephens and Traylor, 1983): collecting locality of C. Kalinowski on left bank of the lower Río Yavarí, 10–15 July 1957.

Santa Cecilia (3°33′S, 72°53′W; Robbins et al., 1991): collecting locality of C. Kalinowski on right (east) bank of Río (or Quebrada) Manití, 27 December 1956–21 January 1957 (Robbins et al., 1991). The Manití is a minor right-bank tributary of the Amazon below Iquitos.

San Vicente (coordinates unknown): collection locality of C. Kalinowski on the Río Yavarí (probably on the left bank between the mouth of the Yavarí-Mirím and the Amazon; Voss and Fleck, 2011), 2 October 1957.

Tahuayo Farm (4°20′S, 73°13′W): inventory site at an abandoned palm farm on the right bank of the Quebrada Blanco (q.v.); surveyed for bats on 19 February 2019. See Materials and Methods for a description of fieldwork this site.

Tapiche (7°12′S, 73°56′W; Vriesendorp et al., 2006): inventory site on right (east) bank of the upper Río Tapiche; surveyed for bats and other mammals by M.L.S.P. Jorge and P.M.V. from 12 to 17 August 2005 (Jorge and Velazco, 2006). According to Vriesendorp et al. (2006), this floodplain site included early-successional riparian vegetation behind the river beach, tall forest on terraces further inland, and an extensive palm swamp (*aguajal*).

Wiswincho (5°49′S, 73°52′W; Pitman et al., 2015): inventory site about 2 km from the left bank of the lower Río Blanco; surveyed for bats and other mammals by M. Escobedo-Torres from 9–14 October 2014 (Pitman et al., 2015).

APPENDIX 2

Expected Species

In addition to bats definitely recorded from the Yavarí-Ucayali interfluve (as documented in our taxonomic accounts), other species with geographic ranges that overlap or adjoin our region (Gardner, 2008c) can also be expected to occur there. These expected species are listed below, together with relevant geographic information.[16] Extralimital localities that fall just outside the fluvial limits of our region are mapped in figure 1.

1. *Centronycteris maximiliani*: A single specimen (MUSM 16464) of this seldom-collected but widespread species was reported from the Reserva Nacional Allpahuayo-Mishana, (RNAM), about 25 km SW of Iquitos on the left ("north") bank of the Amazon (Hice and Solari, 2002).
2. *Diclidurus albus*: A single specimen (AMNH 99310) of this rare but widespread species was collected at Parinari (4°34′S, 74°26′W; Gardner, 2008c; Escobedo and Velazco, 2012) a village on the left (north) bank of the Río Marañón about 93 km NW of Jenaro Herrera.
3. *Diaemus youngii*: Thomas (1928) reported a single specimen of this widespread species from Pebas (3°20′S, 71°49′W; Gardner, 2008c), a village located on the left (north) bank of the Amazon immediately opposite the Yavarí-Ucayali interfluve. Additionally, one specimen was reported from Yarinacocha (8°17′S, 74°39′W; Gardner, 2008c) a locality on the left (west) bank of the Ucayali just south of our region in the department of Ucayali by Sanborn (1949b).
4. *Anoura geoffroyi*: One specimen (LSUMZ 16468) of this widespread species was reported from Balta (10°08′S, 71°13′W; Voss and Emmons, 1996) in the department of Ucayali by Voss and Emmons (1996).
5. *Lichonycteris degener*: One specimen (LSUMZ 12107) of this widespread species was reported (as *Lichonycteris obscura*) from Yarinacocha (8°17′S, 74°39′W; Gardner, 2008c) a locality on the left (west) bank of the Ucayali just south of our region in the department of Ucayali by Gardner (1976).
6. *Lonchorhina aurita*: One specimen (MUSM 17981) of this widespread species was collected at Aguas Calientes (7°11′S, 74°57′W; about 112 km WNW of Tapiche), in the Cerros de Canchaguaya, part of the Sierra de Contamana, in the department of Loreto.
7. *Lonchorhina inusitata*: Previous to its recently reported occurrence in Peru (Mantilla-Meluk et al., 2019), this species was known only from low-elevation localities on the Guiana Shield (in southwestern Venezuela, Guyana, Surinam, and French Guiana) and southward into the Brazilian states of Mato Grosso and Rondônia. The Yavarí-Ucayali interfluve lies between the previously documented distribution of the species and Mantilla-Meluk et al.'s (2019) new Peruvian locality. This species apparently roosts in rocks and caves (Brosset and Charles-Dominique, 1990) so it perhaps occurs in our region only in the Sierra del Divisor.
8. *Lasiurus blossevillii*: Quintana et al. (2009) and Voss and Emmons (1996) reported specimens (e.g., LSUMZ 14312) of this very widespread species from Balta (10°08′S, 71°13′W), over 400 km SE of our region in the department of Ucayali. Although this appears to be the nearest vouchered record, a species provisionally identified as *L. blossevillii* was recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera in 2012.
9. *Cynomops abrasus*: The taxonomy and systematics of this very widespread species was

[16] Escobedo-Torres (2015) listed eight species in addition to those listed here as "expected" in our region (*Pteronotus gymnonotus*, *P. parnellii*, *P. personatus*, *Centronycteris centralis*, *Lasiurus cinereus*, *Eumops bonariensis*, *E. glaucinus*, *E. perotis*), but none is apparently known from the Amazonian lowlands of Loreto or Ucayali departments or from adjacent parts of western Brazil or southeastern Colombia.

reviewed by Moras et al. (2016). Eger (2008) and Medina et al. (2016) reported *C. abrasus* in the departments of Cusco, Huánuco, and Madre de Dios, but it has not yet been reported from Loreto or Ucayali.

10. *Cynomops milleri*: The holotype of this very widespread species (Moras et al., 2018) was collected at Yurimaguas (5°54′S, 76°05′W), a village on the Río Huallaga about 200 km west of our region in Loreto department (Osgood, 1914).
11. *Eumops auripendulus*: Nogueira et al. (1999) reported this widespread species from the Parque Nacional Serra do Divisor in Brazil. Additionally, it is known from Pucallpa (8°23′S, 74°32′W [MUSM 242]) and Colonia Penal Sepa (10°49′S, 73°17′W [MUSM 12748]) in the department of Ucayali, Peru.
12. *Eumops delticus*: A single specimen (CML 7560) of this rare but widespread species was collected in the vicinity of Iquitos (3°48′S, 73°18′W) on the left bank of the Amazon immediately north our region (Díaz, 2011). Additionally, two specimens (MUSM 44156, 44455) identified as *Eumops* cf. *delticus* were recently reported from the Río La Novia Conservation Concession (9°51′S, 70°42′W) south of our region in the department of Ucayali (Ruelas et al., 2018).
13. *Eumops maurus*: A single specimen (CML 7559) of this rare species was collected in the vicinity of Iquitos (3°46′S, 73°18′W) on the left (north) bank of the Amazon immediately opposite our region (Díaz, 2011).
14. *Eumops nanus*: This rare but widespread species has been reported (as *Eumops bonariensis*; Eger, 2008) from the Panguana Biological Station (9°37′S, 74°56′W), about 290 km SW of our region in the department of Huánuco by Hutterer et al. (1995).
15. *Eumops trumbulli*: Specimens of this rainforest species were reported from two localities on the left (north) bank of the Amazon directly opposite the Yavarí-Ucayali interfluve: Leticia (4°09′S, 69°57′W) in the department of Amazonas, Colombia (Eger, 2008), and Boca Río Peruate (3°42′S, 71°29′W) in the department of Loreto, Peru (Medina et al., 2014). Additionally, several specimens have been reported from two localities south of our region in the department of Ucayali: Alto Río Tamaya (8°59′S, 73°19′W; Eger, 2008) and Yarinacocha (8°17′S, 74°39′W; Zamora et al., 2014).
16. *Molossops temminckii*: Hice et al. (2004), Eger (2008), and Ruelas et al. (2018) reported this species from three localities north of our region in the department of Loreto: Reserva Nacional Allpahuayo-Mishana (3°58′S, 73°25′W), Curaray River mouth (2°22′S, 74°05′W; AMNH 71634), and Flor de Yarina, Samiria River (5°02′S, 74°30′W; MUSM 799), respectively. Additionally, Ruelas et al. (2018) reported one specimen (MUSM 44456) collected south of our region in the Río La Novia Conservation Concession (9°51′S, 70°42′W) of Ucayali department.
17. *Nyctinomops macrotis*: This is a very widespread species that occurs from the southern United States to northern Argentina. Although rare in Peru, it has been reported (as *Tadarida molosa*; Sanborn, 1951) from Huajyumbe (13°15′S, 70°30′W; Gardner, 2008c) in Cuzco department and from 12 miles N of Olmos (5°55′S, 79°47′W; Gardner, 2008c) in Lambayeque (Graham and Barkley, 1984). Although these are very distant records, a species identified as *Nyctinomops* cf. *macrotis* was recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera in 2012.
18. *Promops nasutus*: Although this widespread species is not known to occur in Peru (Eger, 2008), a vocalization identified as *Promops nasutus* was recorded using acoustic methods during the CEBIO bat course at Jenaro Herrera in 2012.

APPENDIX 3
Geographic Distribution of Bat Species from the Yavari-Ucayali Interfluvial Fauna

Table entries record documented occurrence of species in four Neotropical rainforest biomes (fig. 38) based on references cited in our species accounts. However, not all of these bats are restricted to rainforest biomes (some species, for example, also occur in the Llanos, Cerrado, Chaco, etc.), so table entries are not necessarily a complete summary of their ecogeographic distributions.

	Rainforest biomes[a]			
	trAn	coVe	Ama	Atl
Cormura brevirostris	X	X	X	
Cyttarops alecto	X		X	
Diclidurus isabella		X	X	
Peropteryx kappleri	X	X	X	X
Peropteryx leucoptera			X	X
Peropteryx macrotis	X	X	X	X
Peropteryx pallidoptera			X	
Rhynchonycteris naso	X	X	X	X
Saccopteryx bilineata	X	X	X	X
Saccopteryx canescens	X	X	X	
Saccopteryx leptura	X	X	X	X
Noctilio albiventris	X	X	X	X
Noctilio leporinus	X	X	X	X
Carollia benkeithi			X	
Carollia brevicauda	X	X	X	X
Carollia perspicillata	X	X	X	X
Desmodus rotundus	X	X	X	X
Diphylla ecaudata	X	X	X	X
Anoura caudifer	X	X	X	X
Choeroniscus minor	X		X	X
Glossophaga bakeri			X	
Glossophaga soricina		X	X	X
Glyphonycteris daviesi	X		X	X
Glyphonycteris sylvestris	X	X	X	X
Trinycteris nicefori	X	X	X	X
Hsunycteris dashe			X	
Hsunycteris pattoni			X	
Hsunycteris thomasi	X		X	

APPENDIX 3 *continued*

	Rainforest biomes[a]			
	trAn	coVe	Ama	Atl
Lionycteris spurrelli	X		X	
Lampronycteris brachyotis	X	X	X	X
Micronycteris brosseti			X	
Micronycteris matses			X	
Micronycteris megalotis	X	X	X	X
Micronycteris microtis	X	X	X	
Micronycteris minuta	X	X	X	X
Micronycteris hirsuta	X	X	X	X
Chrotopterus auritus	X	X	X	X
Gardnerycteris crenulata		X	X	X
Lophostoma brasiliense	X	X	X	X
Lophostoma carrikeri			X	
Lophostoma silvicolum	X	X	X	X
Macrophyllum macrophyllum	X	X	X	X
Phylloderma stenops	X	X	X	X
Phyllostomus discolor	X	X	X	X
Phyllostomus elongatus	X		X	X
Phyllostomus hastatus	X	X	X	X
Tonatia maresi		X	X	X
Trachops cirrhosus	X	X	X	X
Vampyrum spectrum	X	X	X	
Rhinophylla fischerae			X	
Rhinophylla pumilio			X	X
Artibeus concolor			X	
Artibeus lituratus	X	X	X	X
Artibeus obscurus			X	X
Artibeus planirostris	X		X	X
Artibeus anderseni	X		X	X
Artibeus bogotensis		X	X	
Artibeus cinereus			X	X
Artibeus glaucus		X	X	
Artibeus gnomus		X	X	X
Chiroderma trinitatum		X	X	
Chiroderma villosum	X	X	X	X
Enchisthenes hartii	X	X	X	
Mesophylla macconnelli	X	X	X	X
Platyrrhinus angustirostris	X	X	X	
Platyrrhinus brachycephalus			X	

APPENDIX 3 *continued*

	Rainforest biomes[a]			
	trAn	coVe	Ama	Atl
Platyrrhinus fusciventris			X	
Platyrrhinus incarum			X	X
Platyrrhinus infuscus			X	
Sphaeronycteris toxophyllum	X	X	X	
Sturnira giannae			X	
Sturnira magna			X	
Sturnira tildae	X	X	X	X
Uroderma bilobatum		X	X	X
Uroderma magnirostrum	X	X	X	X
Vampyressa thyone	X	X	X	
Vampyriscus bidens			X	
Vampyriscus brocki			X	
Vampyrodes caraccioli		X	X	X
Furipterus horrens	X	X	X	X
Thyroptera discifera	X	X	X	X
Thyroptera lavali			X	
Thyroptera tricolor	X	X	X	X
Thyroptera wynneae			X	X
Eptesicus brasiliensis	X	X	X	X
Eptesicus furinalis	X	X	X	X
Lasiurus ega	X	X	X	X
Myotis albescens	X	X	X	X
Myotis nigricans	X	X	X	X
Myotis riparius	X	X	X	X
Myotis simus			X	
Cynomops planirostris			X	X
Eumops hansae	X	X	X	X
Molossops neglectus			X	X
Molossus coibensis	X	X	X	
Molossus molossus	X	X	X	X
Molossus rufus	X	X	X	X
Promops centralis	X	X	X	

[a] Abbreviations: trA, trans-Andean rainforest; coV, coastal Venezuelan rainforest; Ama, Amazonia; Atl, Atlantic rainforest.

APPENDIX 4

Natural History Monologs about Bats

The following texts are English translations of recorded descriptions of bat natural history by two Matses hunters. The audio files, accompanied by a transcription (in Matses), parsing (segmentation into morphemes, and English glosses of the morphemes), free English and Spanish translations, and annotations (linguistic, ethnographic, biological, and other explanatory notes) can be found in the Endangered Languages Archive at the School of Oriental and African Studies, University of London (https://www.soas.ac.uk/elar/), where they have been accessioned as follows:

Uaqui Canshë, C.N. (2010). DWF1051c: The different types of bats (natural history). *In* D.W. Fleck (researcher), Documentation of the Mayoruna languages.

Jiménez Dësi, L.D. (2010). DWF1055b: Bats (natural history). *In* D.W. Fleck (researcher), Documentation of the Mayoruna languages.

Only the English translations are reproduced below, together with selected annotations (in square brackets or as footnotes). For ease of reading, sentences have been compiled into paragraphs, but this is often arbitrary, and paragraph structure is absent in the archived data. Information that is implied by the context but not explicitly stated is enclosed in parentheses. Italics indicate words spoken by the interviewer (D.W.F.).

Id: DWF1051c.
Title: The different types of bats (natural history).
Narrator: Cesar Nacua Uaqui Canshë.
Context: Prior to this recording, the narrator was asked to list the different types of bats that he had seen or otherwise knew of. Then, D.W.F. asked him to talk about each of the listed bat types, prompting the narrator with a descriptive phrase corresponding to each type.

Tell about bats, first about the blood suckers.[1]
Okay.[2]

The bat bites like this: During the day, the bats that bite are not around. Then, at night, after (people) have gone to sleep, they enter (the houses). Now there are palmwood floors. Not on that type (of floor). They come on the ground well (without making noise), thinking of the ones that they have bitten before, well (quietly), flapping their wings.[3] As if it was quickly tapping (the victim with its snout), sucking the blood, it repeatedly comes to remove bits of flesh. After that one removes a bit of flesh, another one (does it) next. After that one removes a bit of flesh, another one (does it) next. After that one removes a bit of flesh, another one (does it) next.

The blood sucker does not pass up dogs that have had botfly larvae hatch on them, when that blood sucker removes bits of flesh from the noses of all of them (i.e., from many dogs).

There is that other type of bat that is a biter, one that bites intensely. That other type of bat is truly one that repeatedly comes to get blood. Constantly coming to get it (the blood), it repeatedly comes at night to bite, leaving the buttocks (of a person) in bad shape.[4] Now that they (the Matses) wear clothing on their buttocks, that does not happen. The bat comes repeatedly to remove pieces (of flesh), such that the wound heals leaving (the area around the wound) blackish.

That blood-sucking bat is one that bites. The one that bites like that is a black bat.

Did that same kind bite chickens?

What? Another one that is large repeatedly quickly bites chickens on their feet. Right on the feet. It comes and removes bits of flesh from the foot such that there is a lot of blood. When it does that to it, limping, the chicken at

[1] Vampires (Phyllostomidae: Desmodontinae).

[2] Spoken by Cesar, the narrator; henceforth, this speaker's identity will be unmarked in this text.

[3] In other words, when it bites a person, dog, etc., it returns to feed on that same victim.

[4] In other words, it bites people on the buttocks, and because of its anticoagulant saliva, the wound does not stop bleeding after the bat leaves.

its house [i.e., in the chicken coop] ...[5] Once it gets used to (going to that chicken coop), by repeatedly biting the chickens in the same manner, that one, the bat, finishes them off sucking their blood. Also repeatedly biting off bits of the flesh from the chicks, removing (bits of flesh) where their little anuses are, that one kills many chicks.

The bat is one that bites by doing like that. The one that bites, I'm saying. By contrast, others (other bats) are not ones that do like that.

The blood sucker is truly one that does like that. It does not say "(This is) a human."[6] That other bat (i.e., the vampire mentioned first in this narration) is one that, without saying "Oh! it is (too) large (to bite)," repeatedly comes to bite people.

That is truly how that other type of bat is, David.

Yes.

One that truly bites like that.

Tell about the little river bat.

Okay. The river bat is like this, yes:

At dusk, just above the surface of the water, all of them set out, flying as a group along the surface of the water. That one vocalizes saying "[imitation of bat vocalizations]" [imitation of sound of bats flapping their wings].

Do you think that the ones that live on the river are large? Those are small ones. Small, little, those (are).

The ones that are like that, after flying around together many at night, they arrive to hang (roost) where they were hanging before, below an old tree that has fallen over that is stuck above [i.e., a tree that is leaning over, stuck on another tree]. After hanging on below (a leaning tree), they all hang looking at [i.e., oriented toward] the ground, after grabbing on (to the tree) with their feet. They are ones that do not live after making a nest. Their home is under a tree where it is dry. They hang out in the open.

They fly around only right along the surface of the water, only along the surface of the water, along the surface of the water.

Those bats fly around in a group emitting a scent. They are full of their scent, all stinky.

After having flown around as a group like that (the night before), at dusk they fly around over the surface of the water, also where a big deep river curves, repeatedly going along its entire length. Then, as the day is dawning, they arrive to sleep at the same place where they were before.

The bat that is like that is another (type of) bat.

Okay, talk about the plantain eater next.[7]

On the other hand, the plantain eater ...[8]

It becomes dark, like this. Nowadays they are saying "seven (o'clock PM)." After it gets dark, after a little while, they fly around in large numbers [imitation of bats flapping]. After smelling the (ripe) plantains, they fly around the house in large numbers [imitation of bat vocalizations]. As they fly right where they had flown before, without doing anything else (i.e., without wasting time), they eat the (ripe) plantains. In some (plantains) they make holes. Then … [imitation of bat vocalizations].

After being there for a while, again they leave [imitation of sound of bats flying as they exit the house]. While they set out, they pass by defecating [imitation of sound of bat feces hitting the ground]. They have defecated pure plantain!

After perching on top of them (the plantains), they eat quickly. After doing that, again (they come to eat plantains). Then, again (they come to eat) the ones [i.e., the plantains] that have been placed on the ground.[9] They go flying close to the ground [imitation of sound of bats flapping]. They are as if doing it to annoy us, when

[5] Sentence not finished.

[6] In other words, it does not hesitate to bite humans, as a dog or small wild animals might.

[7] Although several species probably eat plantains, this term is typically used to refer to bats that enter Matses houses to eat plantains that have been hung up to ripen. The bats we have found eating plantains in Matses houses are *Carollia* spp., but other phyllostomids probably do so as well.

[8] Sentence not finished.

[9] The Matses hang plantains from walls and rafters to let them ripen. Those are what bats primarily eat, but, as the narrator says, they also eat plantains that have been placed on the floor.

they see plantains [imitation of sound of bats flapping].[10] Constantly coming indoors, they repeatedly come and eat the plantains that have been placed on the ground. Then, after coming slowly and sitting on top (of the plantains), with their wings hanging down at their sides, the bats continually eat the plantains. They are truly ones that by doing that finish off the plantains. The plantain eaters, the bats, finish off all the plantains.

That one is small. It is a dark-colored bat that does like that. Ones that are black/dark-colored. That bat, its wings are thin (-membraned). On the tips of those (wings), there is something for them to hold on with when they hang [i.e., a claw], behind, behind (the wing). Likewise, (it has a claw) where its arm (i.e., its thumb claw) is. The terminal end of its wings come to a point, its foot claws. Also, what it uses to hook on when it hangs are sharp [i.e., the claws on its feet].

The ones that are like that, after making their nest between the layers of thatch of the house, they give birth to their many young. After that, they begin to laugh (vocalize) in large numbers [imitation of bats vocalizing in their nest]. From right there they repeatedly come and eat plantains, after having made their nest there (in the thatch of the roof of the house). After they give birth to its young right there, there are many of its young. They (the young) are very small. They give birth to very many young! They give birth to very, very many. Then [imitation of sound of bat flying], their mother (flies like that). In the morning, upon listening, [imitation of bat vocalizations]. After making a hole in the thatch covering of the apex of the roof, that one gives birth to its young.

The plantain eaters are ones that do like that, David.

Okay. How about the bats that are in new rolled wild banana leaves?[11]

The (ones that are) in new rolled leaves of wild banana plants...[12]

The ones that are in the partly opened soft new rolled leaf of what are called wild banana plants, those first fly halfway up the trees [i.e., in the middle level of the forest] [imitation of bat vocalizations].

Ones that are small. Not large ones [imitation of bat vocalizations].

Those eat many fig-tree fruits, where there are no plantains. What they have eaten piles up (under their feeding perches) right up to here [the narrator shows, holding his hand about 10 centimeters from the ground, how high the pile of food leavings is], fig fruits that they have eaten after going and getting them, what they have made into crumbs, shreds that they have let fall as they eat the peels. The bats eat making big piles (of their leavings). They eat fig fruits and other fruits after getting them and bringing them back (to their feeding perches).

After doing that, back to the same place, in the new rolled wild banana leaves. There are many there, in the new rolled wild banana leaves. Their young are there, too. That's how that other type of bat gives birth, low (close to the ground), the ones that are in new rolled wild banana plants.

There exists that other type of bat that is really one that gives birth like that. That's how much there is (to tell) for that one, the one that gives birth like that (in new rolled wild banana leaves).

Okay. How about the one they call back-striped bat? What is it like?

The one called back-striped bat is like this.[13]

Ṣhokkodo (bananalike) plants, not wild banana plants, while hanging they cut partway through the sides of large ṣhokkodo plants (leaves), until both sides (of the leaf) droop

[10] In other words, rather than going directly to eat the plantains, they noisily fly around.

[11] *Thyroptera tricolor* is the only bat known to roost in the rolled new leaves of *Heliconia* spp. (known as mani pada by the Matses) as well as cultivated bananas, plantains and other monocots with similar leaf morphology.

[12] False start.

[13] The expression "back-striped bat" could obviously refer to multiple unrelated species with striped backs. When Matses are asked about back-striped bats, they often mention that they live in depressions in tree trunks, in which case they are probably referring to *Saccopteryx bilineata* or *S. leptura*. Here, however, the narrator seems to have chosen to talk about a stenodermatine, possibly *Uroderma bilobatum*.

down.[14] When they see that the leaf of the one called "forest ṣhokkodo" plant or of the one called "manioc flour (basket) liner" plant or of the "armadillo (burrow) flooder" plant is good and new, while hanging there, they pierce small holes in its sides until both sides droop down, until it is good [i.e., a good shelter].[15]

The little back-striped bat eats only dicot tree fruits while hanging there in large numbers. They also eat bata tree fruits.[16] That little back-striped bat is truly a bata tree fruit eater.

It does not sleep in termite nests, I'm saying. Its nest is there (in the leaf tent). While hanging in the ṣhokkodo plant, they themselves scratching (holes) using their nails as they know how ...[17]

They don't make the other side (of the leaf) fold down all the way. Their nest that is like that is very good. It is good, dry.

They hang inside the ones that are like that [i.e., the tent nests] looking at the ground (i.e., upside down). The bats are ones that do not hang looking up. They laugh as they look toward the ground [i.e., upside down].[18] They are there flashing.[19] The bats, the ones that are in the ones that are like that [i.e., in the tent nests], are truly ones that appear as if they are laughing.

Did you hear, David?

Yes.

How about the one that is in termite nest holes?

By contrast, a termite nest, the one called termite nest [literally, "wood owner"], a termite nest that is on the trunk of a tree, which is large, one with a large bottom end that is wrapped around a tree trunk.[20] That's where they dig out their hole, large. Could it be what they themselves have dug it out, or (is it) what some bird has dug out? [21] It must be what they themselves dig out.[22] After doing that, they make the hole larger.

In that one (the termite nest roost), (live) big ones, big bats, ones having long wings. Then, after making their nest/home there, they hang inside there.

Then, when people find them, many come out and fly off, during the day [imitation of sound of bats swooping past]. Many exit (the termite nest), when people find them.

They are big bats that are all large. Truly big bats, I'm saying, not little ones.

[imitation of sound of bats swooping] After flying off like that (when disturbed during the day by people), on that same day, they come back to that same one [i.e., to their termite-nest roost] on the same day. Flying in that same manner, the ones that had flown off enter there. Upon looking when they (the people) come back again, they fly off exiting from that same place [imitation of sound of bats flying off].

After that, when it gets dark, they laugh intensely, eating fig tree fruits. As they repeatedly go and get them (the fruits) [imitation of bat vocalizations, imitation of sound of bats flying, imitation of bat vocalizations]. They eat fig fruits actively, not while hanging there (in their sleeping roost), coming to pick them to eat them at a distant place. They actively come and pick fig fruits, fig tree fruits that are in floodplain forest, ones with thick rinds. Many of those big one (bats) come to pick those (fruits) [imitation of bat vocalizations, imitation of sound of bats

[14] As mentioned earlier, mani pada plants are *Heliconia* spp. (Musaceae), whereas ṣhokkodo plants are *Calathea* spp. (Marantaceae).

[15] Ṣhokkodo and tsawes ampukte are names for the same plant; machi ampukte is another, larger, wild banana-like plant.

[16] This term refers to several species of trees, of the genus *Pseudolmedia*, and possibly other genera of the family Moraceae.

[17] Sentence not finished.

[18] In other words, their vocalizations sound like laughter.

[19] As they roost in the somewhat dark nest, their dorsal and facial stripes appear and disappear as they move around.

[20] Probably *Lophostoma* spp., which always roost in hollow termite nests, but possibly also *Phyllostomus hastatus*, which does so occasionally.

[21] The narrator is not sure if the initial hole is made by the bats themselves, or if a bird first digs out the hole to make its nest. The bird that does this is called wis wisëmpi (the brown jacamar, *Brachygalba lugubris*), although perhaps other jacamars also do so.

[22] The narrator concluded this, as he later explained, because birds make their nest with the entrances at the side of the termite nest, whereas the bats' entrance is at the bottom.

swooping out of their roost, imitation of sound of bats flapping].

Those are the size of a nighthawk, very big ones, black ones, ones with long wings, ones with wings as long as a bird's, ones with wings the size of that one's (a nighthawk's) wings. Not like a bird's wings, I'm saying, it is one piece.[23] There are no feathers that can be pulled out. Its big wings are very thin (membraned). The part that it flaps with (its wing membrane) ends where its hand is, very thin. (It is) like the thing for keeping off rain that the non-Indians fabricate that people buy [i.e., like an umbrella]. Doing like that, with their (finger) bones they prepare (extend) their wings well, such that they are good (for flying).

Then, the bats fly around in large numbers stinking intensely [imitation of sound of bats flapping]. While saying "[imitation of bat vocalizations]" they eat their food flying around as a group without sleeping.

The big bats are ones that after eating while flying around without sleeping, go to sleep in the same place where they slept before. They sleep in their same (termite nest) hole, in that same one.

That is how the big bats sleep, David.

Okay.

How about the bat that has a (free) tail?

By contrast, the tailed bat, like this (on) a kuëte çhuda tree ...[24] Since don't you know how the kuëte chuda tree is, such that it has ridges (along its trunk)? In one of those that has gotten stuck as it fell over [i.e., the kuëte chuda tree is leaning at an angle, or horizontally above the ground], in the rifts on the underside of that one, hang many tailed bats.[25]

That one, the other (kind of) bat has a long little stub tail, a long stub tail.[26] That one has its little ears. Its ears. Those have ears that look as they have a spectacle bridge (as a spectacled caiman does), very pretty.[27] The tailed bats are ones that have a nose that sticks up. Another (type of bat), that one is another bat, the one that has a tail.

In the same manner (as the one described above), it does not have feathers that could be pulled out. In the same manner (as the bats that live in termite nests, as described above), they arrange (their wings, spreading them with their fingers). Like an umbrella, they (their wings) are thin, what they flap with, what they flap with at night.

Right there (in the rifts of the kuëte çhuda tree) they give birth to their young, very many. After doing that (giving birth), those, the bats, do not leave their young there. They (the young) hang on (their mother's) venter. There it has its little teats. They don't hang on the other side, on their backs. They themselves pass onto their (mothers') backs (when they get older). (As they pass over to the back) grabbing on like that, their young do not fall off. There is never the opportunity to say "Here a bat's young has fallen." The mother carries them well. They (the young) have their claws, which they use to grab on to her, which they use to grab on to their mother's body.

After doing that (giving birth and taking care of their young), the little tailed bats become very numerous. The bat is one that gives birth like that, in the hole (rift) of the trunk of a tree, in the trunk hole (rift) of the kuëte chuda tree, in the one that is for carving ax handles.[28] Those, the tailed bats, are truly ones that give birth in places like that.

Okay. Tell next about the one that lives in undercut banks of streams.[29]

Those, the ones that are in undercut banks of stream, yes, they begin around this time, at dusk [imitation of sound of bats flying of their roost].

[23] In other words, the wing membrane is one piece, unlike a bird's wing which is composed of many feathers.

[24] Sentence not finished.

[25] Kuëte çhuda or iwi çhuda is a general term for several species of trees that have ridges and deep rifts along the entire length of their trunks.

[26] The term chipidish, here translated as "stub tail," is used for short-tailed species such as tapirs or acouchis.

[27] The narrator might be talking about a molossid with ears connected by skin folds that meet above the eyes.

[28] The Matses use the ridges of these trees for carving ax handles (and the buttress roots for carving canoe paddles). Iwi çhuda is an older name for the kuëte çhuda tree.

[29] Many species of bats roost beneath the undercut banks of streams, so it's not clear what species is meant here.

That one, by contrast (to other bats), confronts (people).[30] That one is one that does not say "(This is) a person (so I will steer away)." They fly in tight circles coming very close, such that it seems that they would pull out one's eyes [imitation of sound of bats flapping].

In that same manner, they fly along the surface of the water, at night, following far the course of the stream [imitation of sound of bats flying]. They fly together up high [imitation of sound of bats flying]. With their perfume smelling oily. I'm talking about their stinky scent. Letting off their scent [imitation of bats flapping].

Then when it is dark, in the same manner [imitation of bats flying]. At dusk they begin to fly over the surface of the water. When the ground is dark (but it is still a bit light) [imitation of sound of bats exiting their roots, imitation of sound of bats flapping, imitation of bat vocalizations, imitation sound of bats flying over the water].

After flying around as a group like that, they go there, where the undercut bank of the stream is. Where the current has dissolved (the ground under) a tree root leaving only fluff (masses of tiny hanging roots), that is where their nest/home is. Many stop to hang there, along its entire length [i.e., along the whole exposed root]. They hang along it like this. They do not hang all spread out. Like this, along a line like this [the narrator makes hand gestures to indicate a single file]. Then, they flash (their teeth) as they perch in a line. They are all there flashing (their teeth). Heads...[31] Those bats that live in undercut banks of streams are there in a group as if they were smiling.[32] With their teeth very white, they look as if they were smiling. Their heads flash from a distance (due to their bright teeth). Those move around (twist and turn).

The bats that live in undercut banks are truly like that.

Right there they give birth to their young, right there. The one that is like that does not live in termite nests. It lives where it has gotten used to living, in the undercut bank.

That one is another bat.[33] A true/actual bat, but another one, I'm saying. That one (is) another one, but a true bat just the same. It does not have a different type of wing. They (their wings) are the same (as those of other bats [i.e., not like bird wings]). Their wings are the same.

Then, they give birth to their young. When they are just born, they hang on the venter (of the mother), on the side where their abdomen is, after grabbing on well. The ones that are like that, their young are pretty. Once they become strong, once they become strong after sucking their mother's teats, once they learn to "crawl," as they say, once they can move on their own, they pass on to the back (of the mother) and hang on her back. Meanwhile, the mother flies/travels [imitation of bat vocalizations]. There/then the young begin to learn. Those, (learn to fly) next. Then, once they become light [i.e., once they learn to fly well], they exit their roosts flying well as a group. Also, the little ones that have not yet become light yet keep on falling to the ground as they fly. After falling down then, after falling down then, after they become light like that, they fly around in a large group [imitation of bat vocalizations].

There another one [imitation of bat vocalizations].

Then, when they see that a person comes close by, they come flying in tight circles, seeming as if they would pull out one's eyes [imitation of sound of bats flapping, imitation of bat swooping close].

They smell strongly. Emitting their scent [imitation of bats swooping around].

After doing that, after flying around at night, in the same manner they stop to hang, in the same manner. In the fluff [i.e., exposed fine roots] that is at the edge of the stream, they twist

[30] In other words, it flies right toward people.

[31] False start.

[32] The narrator is indicating that, for some reason, these bats bare their teeth while roosting.

[33] In other words, not simply the same type of bat described above roosting in a different place.

and turn flashing (their white teeth), without hanging out of order, (hanging) well (in a line).

The bat is one that is like that in the undercut bank of a stream. That is truly how the bat is, that bat.

Well? Did you listen?

Yes. Is there a bat that eats crickets/katydids?

Yes. A big, winged bat. A very large one, one that says "[imitation of bat vocalization]." One had eaten grasshoppers and other (insects), a large grasshopper with big wings.[34] It eats butterflies/moths, too, another bat, a truly big one (does).

Yes.

There are many (insect) wings lying where its (discarded) food is. There are many (insect) wings that it has cut off lying there, ones that have fallen to the ground.

Yes.

That one also eats crickets/katydids. That big one is one that eats all sorts of things.

Birds eat swallowing, swallowing the whole (insect). That one (the bat) does not eat doing it like that, (rather) picking off the wings well. That one eats the whole (body) without letting it fall to the ground.

Yes.

It eats butterflies/moths. Grasshoppers. After that, those grasshoppers. Another one, the one called "howler monkey" (a type of katydid).[35] At night they grab them, after finding them with their eyes.

That's how another bat had eaten, a big one.[36] By contrast, the food [i.e., discarded bits] eaten by the ones that hang on the underside of trees that are on the water [i.e., the "river bat," described above] cannot be seen. Those [presumably the same cricket-eating bats] eat dicot tree fruits, actual dicot tree fruits, fig tree fruits.

By contrast, there another (type of bat) one that is a plantain eater, a bata tree fruit eater.[37] That same one also eats këku tree fruits that are in primary forest, where there are no plantains.[38] They eat everything, eating këku fruits, eating diden këku fruits, eating bata fruits, eating matad fruits, after making a hole in them (i.e., in matad fruits, since they are large fruits).[39] Likewise, that one eats wesnid tëbin tree fruits and others, sweet dicot tree fruits.[40] That one is one that eats like that, the big cricket eater.

Yes.

That big ugly one is one that eats food in primary forest. That one is one that eats food like that. It is a big one that eats bata tree fruits. It does not pass up dicot tree fruits. That one is one that eats all sorts of things, including fig tree fruits and others. It also east grasshoppers, after catching them at night.

That's all (the things) they eat, David.

Okay. Are those all the (types of) bats that you have seen?

Yes. That's how many I have seen, David.

Okay.

Okay.

Id: DWF1055b

Title: Bats (natural history).

Narrator: Luis Dunu Jiménez Dësi.

Context: Prior to the recording, the narrator was asked to list the different types of bats that he had seen or otherwise knew of. Then he was asked to talk about all those bats for the recording. He talked about all the types of bats he had listed, except for vampires, which he described at the end of the recording after D.W.F. reminded him.

Okay, do it.

[34] The narrator knows this by inference, from seeing the discarded wings.

[35] The name of this red katydid is the same as the name of the red howler monkey.

[36] As indicated by verbal evidential inflection (Fleck, 2007), the narrator did not see the bats catch and eat these insects, but rather saw evidence of insectivory (discarded insect wings).

[37] *Pseudolmedia* (Moraceae).

[38] *Couma macrocarpa* (Apocynaceae).

[39] Diden këku = *Parahancornia peruviana* (Apocynaceae); matad = *Naucleopsis* spp. (Moraceae).

[40] Botanical identification is unclear.

Okay.[41] There are many bats, of different types. This is how many there are.

This one, the one that really lives in the undercut banks of streams.

Yet another one, another one is one that lives in the new rolled leaves of wild banana plants.

The one that lives in undercut banks of streams is a black/dark one.

The one that lives in new rolled leaves of wild banana plants is a little one that is a bit whitish. That one is one that sleeps in those, in new rolled leaves of wild banana plants that have not yet unrolled/opened. They are ones that are small.

Yet another one, the one that is in the undivided tips of budëd [*Attalea butyracea*] palms that they have folded down [i.e., have chewed in such a way that the sides of the leaf droop down to form a tent], is always like that. Though it does the same (lives in tents), it is not one whose nose tip points upwards [i.e., it does not have a noseleaf].[42]

Yet another one, the one that lives/is in the hollow of a hardwood tree, the one that lives in the hollow of a fallen one (tree), is another one. Those occur in large groups. Those are ones that are in large groups. That very one, the bat, where its snout is, is it its little leaf? What could it be? Its nose skin flap. That one is one that has a thing like that.[43]

Another one, (lives) in holes in termite nests.[44] By contrast that one is very large. That one is somewhat light colored. Its wings are whitish/somewhat light colored. That one is one that where its snout is has its little noseleaf.

Yet another one, one that (lives) very high up, (roosts) very high up in a tree cavity. That is one that smells more (than other bats), one that smells very bad. That one smells very bad, that one that lives very high up in a big tree. Those occur in large groups. They are many large ones. Those are ones that are very black/dark colored. Its nose sticks up far, its nose skin flap. That one is a black/dark one, a very black/dark one.[45]

Yet another, another (type of) bat, I have not yet seen that one (alive). A very large one, a truly very large one had fallen to the ground, a big bat.[46] That one, one with legs like a person's, which would be just like a little person if it did not have wings, with its head skin like a person's head, had fallen to the ground. It was dying. Why might it have fallen? A very large bat, I have not seen that one (alive). In what type of place might that one live? A very large one had fallen to the ground, a big bat. The Matses call this part here (the narrator points to his upper back), "upper back." That big bat had its upper back just like a person's upper back.[47] I saw a very large one. It had fallen to the ground, one from who knows where. Could it have been that one that was flying above vocalizing in a very deep/low tone? It was saying "[imitation of deep bat vocalizations]." Perhaps it was that one [i.e., a bat of that type]. A very large one, one that fell to the ground. I have not seen that (kind, at any other time). In what sort of place might it live?

Yet another one, those that hang on the river, those that hang on cecropia tree branches that are sticking out of the water, those have stripes (on their back).[48]

Yet another one, which hangs in that same sort of place, on the trunk of cecropia trees, they do not have a pattern (on their back), though they (otherwise) look the same (as the one mentioned in the preceding sentence). Although those look like those, they are not those [i.e., not the same type], since they do not have stripes.[49]

[41] Spoken by the narrator; henceforth, this speaker's identity will be unmarked in the text.

[42] All bats known to inhabit leaf tents are phyllostomids, so either the narrator is mistaken or he simply failed to notice the noseleaf.

[43] The narrator is evidently referring to some kind of phyllostomid, but the information provided is too vague for identification.

[44] As above, either *Lophostoma* spp. or *Phyllostomus hastatus*.

[45] As above, another unidentifiable phyllostomid.

[46] Possibly *Vampyrum spectrum*.

[47] All bats have dorsal thoracic musculature that looks somewhat human, but most bats are furry, so this resemblance is normally concealed. Perhaps this bat had very sparse dorsal fur.

[48] Clearly *Rhynchonycteris naso*.

[49] Another (unstriped) species of emballonurid?

Though they hang in the same type of place, the other bats were striped.

That's how many (types of) bats there are. There are many bats, of different types.

Another one, (a) red (one), I have not seen that one (well). At (the Matses village of) Puerto Alegre I saw it. It had fallen to the ground, a bright red one, a bright red one.[50] I have not seen that one [i.e., have not seen its habits]. In what type of place could that one live? That one, not being very large, was a medium-sized bat. The one I'm saying that I saw was not very large. That one, the red bat, was not very large.

Yet another one, another bat, that one is also one that is inside tree hollows. Another bat, one that has a tail.[51] Then, the one that has a tail is also one that gives birth to its young where the roof of the house is, in the house roof. They vocalize saying "[imitation of bat vocalizations]." Those vocalize a lot [i.e., because they are many]. Those live in large groups, the ones that have a (free) tail. Those have a long tail. Other bats, ones that likewise live in tree cavities, have a short little tail. While the other (type of bats' tails) are long, others are short, short tails. Those (the ones with free tails) are black/dark colored. That other bat with a (free) tail was black/dark colored. But that one, another (type), that bat was sort of brownish. The ones that are like that, their tails are short, while others' [i.e., of the other type of bat] are long.

Those bats exist. That's how many there are.

Another bat would seem to be one that eats fish.[52] Where could that one live? Those fly by very quickly, very quickly. Those fly by very quickly, the ones that fly along the surface of the water. Those fly by saying "[imitation of bat flapping, imitation of bat swooping]." I have not seen in what sort of place that one lives. In what sort of place could they live? There are many of those at the river/stream. There were many of the ones that do like that [i.e., that fly around in large groups]. At the river/stream they eat young fish. After catching small ones (fish) they eat them. They fly very fast. I have not seen those after catching them. What could they look like?

Another one, another bat, another little bat had a white/light-colored neck here [the narrator points to his neck].[53] I have not seen in what sort of place that one lives.

That's all the ones that I have seen, David.

Okay. Have you told about the one that sucks blood?

Oh, that one, the one called "blood sucker," is not very large, not very large.[54] That one is one that that also sucks the blood of dogs that are curled up [i.e., sleeping] outdoors. That one looks just like a (regular) bat. It is one that where its nose is, it has its little flap of skin.' A nose-skin-flap bat. That one is a nose-skin-flap bat, the blood sucker. That one sucks the blood of dogs and other animals.

That's all, David.

Okay.

[50] Possibly *Lasiurus blossevillii*, the only bright-red bat that might occur in our region.

[51] The narrator is surely referring to free-tailed bats (molossids), which are known to roost in thatch.

[52] The narrator is almost certainly referring to *Noctilio leporinus.*

[53] Perhaps *Lampronycteris brachyotis*?

[54] Surely *Desmodus rotundus*, because other vampires feed on birds

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On the cover: Roosting group of *Lophostoma silvicolum* in an arboreal termite nest at Jenaro Herrera, Loreto, Peru. Photo by Marco Tschapka.